A COGNITIVE NEUROSCIENCE EXAMINATION OF EMBODIED COGNITION

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by

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ABSTRACT

Embodied cognition theorists suggest that cognition is bodily based and that the brain developed due to interaction with the environment, and thus evolved to facilitate sensorimotor processing. As such, one goal of embodied cognition research is to determine how the interaction between the body and the environment affects the storage and processing of semantic information. Recent neuroimaging research has shown that the sensorimotor and premotor cortices are activated somatotopically when responding to action-related stimuli. In addition, behavioural research has provided evidence in support of the theory of embodied cognition, in that the sensorimotor properties of a stimulus have been shown to affect performance on language tasks. The goal of the current research was to provide a novel and comprehensive examination of the theory of embodied cognition through the combination of multiple experimental paradigms.

Several functional magnetic resonance imaging and behavioural experiments on healthy participants were carried out, as well as a behavioural study of two individuals who have undergone either a left or right hemispherectomy. The results from the functional neuroimaging experiments demonstrated that there are common regions of activation between motor movements and semantic processing, whereby sensorimotor and premotor regions that are responsible for arm and leg motor movements are also recruited when responding to arm- and leg-related action semantic knowledge. Thus these results are consistent with the theory of embodied cognition, suggesting that the motor system is involved in the processing of actionrelated semantic information. The behavioural results were also consistent with previous research showing that pictures have privileged access to action-related semantic knowledge. Additionally, the behavioural results with hemispherectomy patients provided evidence regarding the necessity versus sufficiency of the left and right hemispheres when responding to arm- and leg-related semantic knowledge. Finally, given that words rated as higher in body-object interaction were responded to faster than words rated as lower in body-object interaction, these results show evidence that language processing is grounded in bodily interaction and sensorimotor processing. Together, the results further advance the theory of embodied cognition, and moreover, provide an in-depth analysis of how arm- and leg-related stimuli are processed dependent upon presentation format.

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DEDICATION

I would like to dedicate this dissertation to my Aunt Patti. You were there when I began this journey and unfortunately were not here to see this chapter close. You told me to follow my dreams, and provided me with the support to do that. I will forever be grateful for the nights on your deck where you told me to follow my heart no matter how bumpy the path may be. You helped shape me into the person I am, you taught me what integrity was, and made sure that in everything I did, I did with integrity. You taught me to respect everyone and everything I do, and how to be courageous in life. I will forever hold these beliefs and values near my heart, and will take them with me wherever I go. Without your loving support, I could not have fulfilled this dream.

"Wherever you are and wherever you go, there's always gonna be some light" (Meatloaf, 1977).

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LIST OF ABBREVIATIONS

ACC	Accuracy
ACE	Action-sentence compatibility effect
AD	Alzheimer's disease
AG	Angular gyrus
ANOVA	Analysis of variance
BOI	•
BOLD	Body-object interaction
	Blood oxygen level dependent
CBD	Corticobasal degeneration
CG	Cingulate gyrus
DLPFC	Dorsolateral prefrontal cortex
fMRI	Functional magnetic resonance imaging
HRF	Hemodynamic response function
IFG	Inferior frontal gyrus
ITG	Inferior temporal gyrus
KDT	Kissing and dancing test
LDT	Lexical decision task
LOG	Lateral occipital gyrus
M1	Primary motor cortex
MEG	Magnetoencephalography
MFG	Middle frontal gyrus
MND	Motor neuron disease
MNS	Mirror neuron system
MSe	Mean square error
MSEC	Milliseconds
MTG	Middle temporal gyrus
PD	Parkinson's disease
PET	Positron emission tomography
PFN	Parietal-frontocentral network
PLDT	Phonological lexical decision task
PPT	Pyramids and palmtrees test
PSS	Perceptual symbols systems
RT	Reaction times
ROI	Region of interest
rTMS	Repetitive transcranial magnetic stimulation
SCT	Semantic categorization task
SD	Standard deviations
SFG	Superior frontal gyrus
SG	Supramarginal gyrus
SLDT	Semantic lexical decision task
SMA	Supplementary motor area
SPL	
STG	Superior parietal lobule
	Superior temporal gyrus
TDR	Total duration to respond
TMS	Transcranial magnetic stimulation

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CHAPTER 1

AN INTRODUCTION TO EMBODIED COGNITION

Much cognitive neuroscience and psychological research has been done with the goal of understanding how semantic memory processes work and what brain regions are responsible for processing such information. Semantic memory refers to an individual's knowledge of words, concepts, symbols and objects (Tulving, 1972), and moreover has been defined as an individual's "knowledge about the world" (Martin, 2007, pg. 26). Early research investigating semantic memory examined the processing of semantic knowledge in brain-damaged patients who had impairments in either the retrieval or storage of semantic information. In an early account, Warrington (1975) described three patients with diffuse cerebral lesions who presented with selective semantic impairments. Specifically, these patients showed no evidence of difficulties in the processing of perceptual information (e.g., patients had intact classification of objects into the same perceptual categories such as determining whether conventional and unconventional views of photographs were the same object, and furthermore, had intact expressive speech and comprehension for syntax), but showed an impairment in retrieving semantic knowledge about objects and words (e.g., were unable to retrieve knowledge about the associations and attributes of objects and words). Hart and Gordon (1990) described three aphasic patients who, in the absence of any perceptual deficits, presented with deficits in semantic comprehension tasks (e.g., deficits in subordinate categorization, single word meaning, and property judgment tasks) that were associated with damage to the left posterior temporal lobe and a small portion of the left inferior parietal lobe. Additionally, Hodges, Patterson, Oxbury, and Funnell (1992) showed a severe impairment of semantic memory in five patients with semantic dementia that was associated with damage mainly to the left temporal lobe. These five patients had severe deficits in the ability to produce exemplars of specific semantic categories (e.g., animals and vehicles), impaired picture naming, difficulties generating verbal definitions of items, and errors in matching pictures with the spoken definitions of the objects. Together, these results demonstrate that damage to the left temporal, parietal and frontal brain regions responsible for the storage and retrieval of semantic information are associated with impairments in the processing of semantic knowledge.

Given that damage to these specific brain regions has been associated with impairments in the processing of semantic information, one aim of cognitive neuroscience research has been

to determine which brain regions are activated in healthy individuals during the processing of semantic information. To examine this, cognitive neuroscience research has used neuroimaging methods (e.g., positron emission tomography (PET) and functional magnetic resonance imaging (fMRI)) to investigate which brain regions are involved when healthy participants respond to tasks that target semantic knowledge. Such research has shown a distributed network of activation encompassing mainly the left temporal, occipito-temporal, parietal, and prefrontal regions during the processing of semantic information (Martin, 2007; Martin & Caramazza, 2003), which is consistent with the regions implicated in patient studies. For example, the retrieval of color information has been shown to activate the left temporal cortex (Chao & Martin, 1999), while animal naming has been shown to activate the bilateral ventral temporal lobes and left medial occipital lobe (Martin, Wiggs, Ungerleider, & Haxby, 1996). In addition, the viewing and naming of pictures of tools has been shown to activate the left premotor cortex, middle temporal gyrus and posterior parietal cortex (Chao & Martin, 2000; Martin et al., 1996), while the silent naming of tool uses activate the left dorsal and ventral premotor cortex and supplementary motor area (Grafton, Fadiga, Arbib, and Rizzolatti, 1997). Furthermore, Martin, Haxby, Lalonde, Wiggs, and Ungerleider (1995; also Martin et al., 1996) have shown that the generation of action-words activates the left middle temporal gyrus. Taken together then, these neuroimaging results support a network of regions in the left hemisphere which are broadly consistent with the regions implicated in the earlier patient research.

Traditional Models of Semantic Memory

Before discussing the theories of semantic processing it should be noted that the terms *semantic and conceptual* will be used interchangeably, given that different authors refer to conceptual representations (e.g., Barsalou, 1999; 2008a; 2008b; Gallese & Lakoff, 2005), while others refer to semantic representations (e.g., Chao & Martin, 2000; Martin & Chao, 2001; Martin, 2007). For example, the theories discussed tend to use the term conceptual representations (e.g., Barsalou, 1999), whereas experimental studies tend to use the term semantic representations (Hauk, Johnsrude, & Pulvermuller, 2004; Martin, 2001; 2007), while some studies use both terms (e.g., Tettamanti et al., 2005). It is clear that the authors from these different research literatures are referring to the same underlying thing when using the terms semantic or conceptual: the meaning of words, pictures, and their referents.

In traditional models of semantic representations, conceptual knowledge is stored in abstract amodal systems, whereby representations are symbolic and abstract (Mahon & Caramazza, 2008; Pylyshyn, 1984; reviewed by Gallese & Lakoff, 2005), with no real relation between the conceptual representation and the referent of that representation (Zwaan, 1999). Amodal symbol system theorists further assume that conceptual representations and perceptual systems, including sensory and motor information, are separate and independent from one another (Mahon & Caramazza). Furthermore, Tulving (1972) suggests that although the input to semantic memory is perceptual, the perceptual properties are not stored in semantic memory. As such, in amodal symbol systems there is no relation between the original perceptual experience and conceptual symbols or representations (Barsalou, 1999). Instead, perceptual states are encoded and transduced into a new representation, and each new experience is encoded into a new abstract representation (Pylyshyn, 1984; and as reviewed by Barsalou, 1999; Barsalou, Simmons, Barbey, & Wilson, 2003), thus requiring no simulation of the perceptual, or sensorimotor, experience when retrieving the concept (Mahon & Caramazza, 2008; Pylyshyn, 1984). However, according to Barsalou (1999; see also Barsalou, 2008a; 2008b; Barsalou et al., 2003) there are many challenges to the traditional amodal view of conceptual representations. One major challenge to this model is that "there is little direct empirical evidence that amodal symbols exist" (Barsalou, 1999, pg. 579; 2008b; Barsalou et al., 2003). Instead, support for amodal theories is provided post-hoc by fitting empirical results to the theory (Barsalou, 1999; 2008b; Barsalou et al., 2003). Second, results from neuroimaging studies challenge the idea that conceptual information is stored in abstract amodal systems separate from perceptual, sensorimotor systems (Barsalou, 1999). Rather, such research has shown evidence that conceptual representations are grounded in sensorimotor processing, whereby brain regions that encode sensorimotor information have been shown to be activated during the retrieval of conceptual representations (Barsalou, 1999). That is, the retrieval of conceptual representations requires at least partial simulation of the perceptual states that they were experienced in, and hence, retrieval of the conceptual representation activates the sensorimotor regions associated with that experience. A third challenge to amodal theories is that they cannot provide an answer to how perceptual symbols are "mapped onto abstract amodal symbols", and how amodal symbols are "mapped back onto perceptual states" (Barsalou, 1999, pg. 580). That is, if there is no relationship between perceptual states and amodal systems, how does one understand the

perceptual meaning of a concept? Finally, amodal systems do not depict how amodal symbols are "comprehended in the absence of physical referents" (Barsalou, 1999, pg. 530). In particular, if there is no relationship between concepts and perceptual events, how does one derive the meaning of a concept without the concept being grounded in some experience? Take for example a ball, if there is no relationship between a perceptual, or sensorimotor, experience and the conceptual representation of the ball, then how does an individual understand how to use a ball, or furthermore, describe how to interact with a ball. Given these challenges, new theories of conceptual processing suggest that conceptual representations are grounded in perceptual and sensorimotor systems, and thus suggest that perceptual and conceptual representations are not stored in separate, independent systems (Barsalou, 1999; 2008b; Fischer & Zwaan, 2008; Gallese & Lakoff 2005; Zwaan, 1999)

The Theory of Embodied Cognition

Recently new theories of semantic processing have been developed with the goal of providing a more thorough, and empirically supported, understanding of how conceptual information is stored and retrieved. One such theory of semantic processing that has been gaining support is the theory of embodied cognition. Embodied cognition theorists suggest that conceptual representations are grounded in perceptual, or sensorimotor, systems (Barsalou, 1999; 2008b), and furthermore, that the mind is shaped by the physical experiences the body has when interacting with the world, and are thus interested in determining how these physical experiences with the environment shape conceptual representations (Gibbs, 2006; Wilson, 2002). As such, the goal of individuals examining the theory of embodied cognition is to determine how the interaction between the body and the environment shapes the development, organization, and processing of the human brain, and how this interaction affects the storage and processing of conceptual information (Barsalou, 1999; Gibbs, 2006; Siakaluk et al., 2008a; 2008b; Wilson, 2002).

Early work by Allport (1985) suggested that there is a notable link between an individual's sensorimotor experiences and the neural processes and conceptual representations of those sensorimotor experiences. Barsalou (1999) furthered this idea with the development of the Perceptual Symbols Systems (PSS) theory. In the PSS Barsalou suggests that there is a strong relationship between an individual's perceptual experiences and his or her conceptual representations. Whereas in amodal symbol systems theories, perceptual symbols and conceptual

representations are separate or independent, in the PSS theory, perceptual symbols, or experiences, shape conceptual representations. That is, the perceptual symbols or representations of an experience are encoded in the brain, these representations form a conceptual simulation of that experience, and when an individual retrieves information about a concept, the perceptual symbols (or experiences) associated with the concept are simulated (Barsalou, 1999). As such, conceptual information is grounded in perceptual, or sensorimotor, experiences that are simulated when re-enacting information about a concept or conceptualization (see also Barsalou, 2009). Moreover, such simulations take place during language processing, whereby during language comprehension, the perceptual symbols must be simulated to understand the meaning of language (Barsalou, 1999). The idea that understanding a concept requires the simulation of the perceptual, or sensorimotor, experiences associated with a concept has become one of the main tenets of embodied cognition. However, it should be noted that with respect to conceptual representations being grounded in perceptual experiences, it is not just bodily experiences that are simulated when retrieving conceptual information (Barsalou, 2008b). Rather, conceptual information is also grounded in other forms of experience not relevant to the body, such as perceptual characteristics like colour or situated actions (Barsalou, 2008b; Barsalou et al. 2003). Nevertheless, most research on embodied cognition is interested in understanding how bodily states, or environment-body interactions, affect conceptual representations.

Accordingly, embodied cognition theorists argue that the storage of conceptual information overlaps with an individual's sensorimotor system (Gallese & Lakoff, 2005; Figure 1). That is, the meaning associated with conceptual information is acquired through sensorimotor experiences and are represented in proximity to the same sensorimotor regions that the perceptual event was experienced in (Barsalou, 1999; 2008b; Gallese & Lakoff, 2005; Fernandino & Iacoboni, 2010). Thus, conceptual information is represented in the same brain regions that are activated when retrieving information about those conceptual representations (Aziz-Zadeh & Damasio, 2008). The neural mechanisms responsible for perception and action are recruited during language comprehension (Rueschemeyer, Lindemann, Van Elk, & Bekkering, 2009); and it has therefore been suggested that activity within the motor system may be an essential component of language comprehension (Fischer and Zwaan, 2008). That is, language comprehension requires that the neural resources used to encode a representation be activated when accessing the meaning of the representation; and furthermore, since these

representations are grounded in perceptual systems, understanding the meaning of a conceptual representation should activate the perceptual and action (or motor) systems.

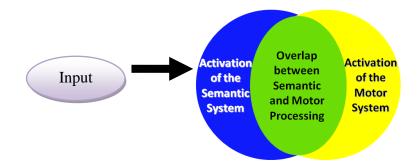


Figure 1: A Conceptual Model of the Embodied Theory of Semantic Memory. Semantic processing overlaps with motor processing, showing that the motor regions are required when simulating action-related semantic representations. This figure illustrates that the same regions are activated during a semantic task and a motor task. It should be noted, as pointed out by my external examiner, that this figure represents a softer version of the theory of embodied cognition, while a harder version of the embodied cognition theory would represent total overlap between the semantic and motor systems.

Taken together, according to embodied cognition theorists, conceptual information is grounded in sensorimotor processes, and thus the sensorimotor regions that encode conceptual knowledge are involved in the retrieval of conceptual knowledge. Furthermore, simulation of the perceptual, or sensorimotor, experiences associated with a conceptual representation must occur during language comprehension. As such, this theory strongly differs from traditional amodal theories, in that in embodied theories a strong link exists between perceptual experiences and conceptual representations.

It is important to note that there are some criticisms to embodied cognition theories in the literature, and thus to provide a thorough examination of embodied cognition, the disembodied cognition perspective needs to be discussed. The critics of embodied theories have proposed that the motor system is activated separately from the semantic analysis of a stimulus and is not required for semantic processing (Caramazza, Hillis, Rapp, & Romani, 1990; Mahon & Caramazza, 2005; 2008; Figure 2). Theorists who support the disembodied view suggest that

conceptual information is first activated, followed by spreading activation to the motor regions. Thus, although both conceptual and motor regions may be activated when processing conceptual information, processing occurs in conceptual regions which then spreads into the motor regions (Mahon & Caramazza, 2008). As such, conceptual processing is not associated with simulation of sensorimotor experiences, and moreover, is not a requirement to understand the meaning of a conceptual representation (Mahon & Caramazza, 2005; 2008). Evidence in favour of the disembodied account comes from apraxia patients who are impaired when using objects, but can name and pantomime the use associated with an object, and vice versa (Negri et al., 2007). This suggests that although there is damage to the motor regions, action-related language is still intact (and vice versa). However, it should be noted that the patients examined by Negri and colleagues have lesions that are not restricted to the motor regions, but rather are wide-spread including regions outside the motor system (e.g., the temporal lobe). Nevertheless, disembodied theories suggest that activation in the premotor regions must be due to spreading activation from other regions after the semantic processing of a stimulus. That being said, even though the disembodied perspective can provide a plausible explanation as to why we see motor activation during conceptual processing, there is overwhelming evidence that the sensorimotor and premotor cortices involvement during the processing of action-related semantic information is more than simply due to spreading activation (as described below). This dissertation will further examine the processing of action-related stimuli in order to test and develop the embodied theory, and will discuss challenges to this theory further in the General Discussion.

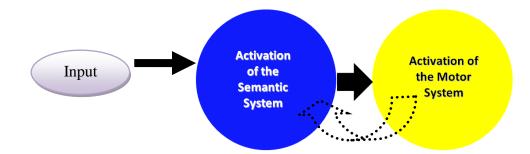


Figure 2: A Conceptual Model of the Disembodied Theory of Semantic Memory. During semantic processing, although activation occurs in both the semantic and motor systems, activation in the motor system occurs after semantic analysis of a stimulus. That is, semantic information is first activated, and then the motor regions become activated. The solid arrow represents the spread of activation from the semantic system to the motor system. Thus, although both semantic and motor regions are activated, the semantic system is activated first, followed by activation in the motor system. However the motor system is not required during the processing of semantic action-related representations. Furthermore, activation occurring in the motor system can also result in a spread of activation back to the abstract semantic representation (as shown by the dashed arrow).

Patient Data in Favour of Embodied Cognition

Previous research examining the processing of action-related language in patient populations has shown evidence in support of embodied cognition (Bak, O'Donovan, Xuereb, Boniface, & Hodges, 2001; Bak & Hodges, 2004; Boulenger et al., 2008; Cotelli et al., 2006a; 2006b). For example, patients diagnosed with motor neuron disease (MND) have shown evidence of an impairment during the processing of verbs, which serve to represent actionrelated language in all known languages. MND is characterized by widespread cortical atrophy mainly in the fronto-temporal regions that causes impairments in motor functioning, and is associated with impairments in verb naming and comprehension, whereas noun naming and comprehension remain intact (Bak et al., 2001). Bak and Hodges (2004) examined the processing of verbs in 7 patients with MND and again found patients to be more impaired at producing and comprehending verbs compared to nouns. As a more comprehensive examination of action processing, three of their patients were also administered the Pyramids and Palmtrees Test (PPT) and Kissing and Dancing Test (KDT). The PPT consists of triplets of pictures of objects, and requires patients to choose which picture of an object best matches the target object (that is, is part of the same semantic category). The KDT, on the other hand, consists of triplets of pictures of actions and requires patients to choose the picture of an action best representing the action of the target picture. All three patients with MND showed greater impairment on the KDT (action semantic decision) compared to the PPT (semantic category decision), which suggests a greater impairment of action-related knowledge than general semantic knowledge.

This effect has also been demonstrated in patients with corticobasal degeneration (CBD), which is characterized by asymmetric (left greater than right) cortical atrophy of the bilateral premotor cortex, superior parietal lobes, and striatum (Cotelli et al., 2006a). The authors found that patients with CBD showed a greater impairment for the naming of pictures of actions compared to the naming of pictures of objects (Cotelli et al., 2006a). Moreover, these patients showed a greater deficit in the naming of actions representing a manipulation compared to nonmanipulation action. Additionally, Cotelli et al. (2006b) examined action and object naming in patients with Alzheimer's disease (AD), as action/verb naming has previously been found to be more difficult than object naming in these patients. Lesion and imaging studies on healthy participants have shown that the left prefrontal cortex plays an important role in the ability to name actions/verbs (Daniele, Giustolisi, Silveri, Colosimo, & Gainotti, 1994), and has been found to be damaged in AD (Cotelli et al., 2006b). Given the damage to the left prefrontal regions and the associated deficits in action/verb naming in AD, Cotelli et al. (2006b) sought to examine whether applying repetitive transcranial magnetic stimulation (rTMS) to the dorsolateral prefrontal cortex (DLPFC) could improve performance on action verb naming in AD patients. Previous research on healthy participants has shown that the application of rTMS to the left DLPFC facilitates action-verb processing (Cappa, Sandrini, Rossini, Sosta, & Miniussi, 2002). Furthermore, Cappa et al. found a greater facilitation in action-verb processing when rTMS was applied to the left compared to the right DLPFC. Cotelli et al. (2006b) found that when rTMS was applied to the left and right DLPFC, patients with AD showed better performance when naming action verbs (greater number of correct responses) than compared to sham stimulation (that is, no rTMS was applied). The authors suggest that the facilitative effect of bilateral stimulation found in AD patients, was due to a compensatory mechanism, whereby when damage occurs in the left hemisphere, the right hemisphere is recruited. However, when rTMS

was applied to either the right or left DLPFC, there was no effect of stimulation on the accuracy of naming nouns. Thus, given the improvement in processing of action verbs when rTMS was applied to the DLPFC, the authors suggest that this region plays an important role in the processing of action verbs.

Finally, Boulenger et al. (2008) found that patients diagnosed with Parkinson's disease (PD), which is characterized by damage to dopamine pathways in regions that control motor functioning, also show deficits in action-verb processing. That is, when Parkinson's patients are in the 'off' phase of treatment (when patients are not receiving dopamine treatments), they are impaired at responding to action-verbs, but show no impairment in responding to nouns (Boulenger et al., 2008). In one experiment, PD patients completed a lexical decision task ("decide whether the letter string is word versus nonword?") where the stimuli consisted of a noun, verb, or pseudo-word that was preceded by either: 1) a masked identical prime of the same action-verb, non action-related noun, or pseudoword, or 2) a non-repeated masked prime that consisted of a meaningless consonant string. For PD patients in the 'off' phase of treatment, there was a priming effect for nouns that was comparable to controls, whereas for action verbs, there was no effect of priming. However, when PD patients were in the 'on' phase of treatment (when patients were receiving dopamine treatments), a priming effect was shown for action verbs. Taken together, these studies suggest that damage to motor regions and pathways are associated with deficits in the production and comprehension of action-related stimuli, suggesting that the motor system plays a role in the ability to process action-related language. Behavioural Support for Embodied Cognition

Previous behavioural research has also provided support for the theory of embodied cognition. Specifically, behavioural research has shown evidence that language processing and comprehension is grounded in bodily interaction. For example, Glenberg and Kaschak (2002) had participants judge the sensibility of sentences ("does the sentence make sense?") that implied a direction either away from the body (e.g., "Close the drawer" suggests movement in a direction away from the body), toward the body (e.g., "Open the drawer" suggests movement towards the body), or abstract/non-sense sentences (e.g., no direction implied). To make the sensibility judgments participants had to press a 'yes' or 'no' button with their dominant hand. Participants were assigned to the 'yes is far' condition, where the 'yes' button was away from the body and the 'no' button was near the body, or the 'yes is near' condition, where the 'yes' button was near

the body and the 'no' button was away from the body. The authors hypothesized that since language meaning is grounded in bodily interaction and is action-based, then the sentences should afford an action either toward or away from the body. That is, the opening of a drawer should simulate an action towards the body, whereas the closing of a drawer should simulate an action away from the body. Thus, if the meaning of the sentence simulates an action towards the body, the affordance of an action towards the body should interfere with responding when participants have to respond using the yes button that is further away from the body, then the affordance of an action away from the body should interfere with responding when participants have to respond using the yes button that is closer to the body (the 'yes is far' condition). On the other hand, if the sentence the interfere with responding when participants have to respond using the yes button that is closer to the body (the 'yes is near' condition). Glenberg and Kaschak termed this interaction, the action-sentence compatibility effect (ACE). The authors found support for the ACE, whereby showing that sentence comprehension can either facilitate (congruent implied action and button response), or interfere with (incongruent implied action and sentence), responding when an individual is required to make a physical response.

Glenberg and Kaschak (2002) sought to replicate these results in a follow-up experiment. In the replication experiment, the same paradigm was used as described above, but participants were required to respond with their non-dominant hand. In another experiment, participants did not have to move their hand to respond, but rather used their left index finger to respond 'yes' and their right index finger to respond 'no'. In the first replication experiment using the non-dominant hand, the authors found support for the ACE effect, whereby the implied action in the sentence either facilitated (congruent implied action and button response) or interfered (incongruent implied action and button response) with responding. However, when participants were not required to move their hand to respond, no ACE was found. Thus these results provide support for the hypothesis that meaning and language comprehension are grounded in bodily actions (Glenburg & Kaschak). Specifically, these results show that when participants have to move a body part to respond, the action implied by the sentence affords an action to the participant that can either facilitate or interfere with responding; however, when no action is required, the action of the sentence does not affect responding.

The idea that language is grounded in sensorimotor processing has been further supported by Siakaluk et al. (2008a) who examined how sensorimotor information affects the recognition

of words. Siakaluk and colleagues developed body-object interaction (BOI) ratings in order to examine how sensorimotor knowledge (or the degree of embodiment of an object) affects word recognition. BOI ratings were collected by having participants rate the "ease or difficulty with which a human body can physically interact with each word's referent" (pg. 436). Words that were rated as high in BOI had a greater amount of sensorimotor knowledge associated with them, whereas words that were rated as low in BOI had less sensorimotor knowledge associated with them (Siakaluk et al.). Participants completed variants of the lexical decision task, and words that were rated as higher in BOI were responded to faster. Siakaluk and colleagues suggest that high BOI words have a greater amount of sensorimotor knowledge associated with them, which activates "richer semantic representations" (pg. 440) than low BOI words, allowing participants to respond faster. However, Siakaluk and colleagues propose that these tasks did not target semantic information, but rather targeted orthographic and phonological processing. As such, Siakaluk et al. (2008b) sought to extend these findings by examining the effect of sensorimotor knowledge on responding in tasks that target semantic knowledge.

To examine this, Siakaluk et al. (2008b) used a semantic categorization task (SCT) and semantic lexical decision task (SLDT). In the SCT, participants were required to decide whether each word was easily imageable or not easily imageable. For both experimental conditions, words rated as high in BOI were responded to faster and more accurately than words rated as low in BOI. These results suggest that semantic processing is facilitated when words have richer sensorimotor representations (Siakaluk et al., 2008b). In the SLDT, participants were required to make a lexical decision ("Is the letter string a word or not?"), followed by a semantic decision ("Decide whether the word is easily imageable"), to determine whether the BOI ratings of a word affects processing when the task targets semantic and orthographic representations. Siakaluk et al. found that in both tasks that targeted semantic knowledge, words rated as higher in BOI were responded to more quickly than words rated as lower in BOI. Taken together, these results suggest that when words have greater sensorimotor knowledge associated with them, they activate "richer semantic representations" (Siakaluk et al., 2008a, pg. 440; Siakaluk et al., 2008b, pg. 600), allowing one to respond more quickly and accurately.

Together, the findings from Glenberg and Kaschak (2002) and Siakaluk et al. (2008a; 2008b) provide support for the theory of embodied cognition. Specifically, these studies demonstrate that the sensorimotor information associated with a sentence/word influences

responding; and furthermore, suggest that the degree of embodiment of a stimulus affects semantic processing, whereby individuals are able to respond faster and more accurately to stimuli that are more embodied.

Neuroanatomical Support for Embodied Cognition: Somatotopic-Semantic Processing

Recently, cognitive neuroscientists have sought to determine whether there is neuroimaging evidence in favour of the sensorimotor system being involved in semantic processing. As such, one goal of cognitive neuroscience has been to determine whether the sensorimotor and premotor regions are activated during the processing of action-related semantic knowledge (Willems & Hagoort, 2007). A second goal has been to determine whether sensorimotor regions are activated automatically when processing action-related stimuli, or rather following the semantic analysis of such stimuli. According to cognitive neuroscientists examining the processing of action-related semantic information, evidence of somatotopicsemantic activation in the sensorimotor and premotor cortices provides support for the idea that action-related semantic knowledge is grounded in action and perceptual systems (Barsalou, 2008b; Boulenger, Hauk, & Pulvermuller, 2009; Pulvermuller, 2005). That is, if the sensorimotor and premotor regions are activated in a somatotopic fashion, much like Penfield's map of the sensory and motor homunculi (Figure 3), when participants respond to effector-specific actionrelated stimuli, then this would provide support for the theory of embodied cognition.

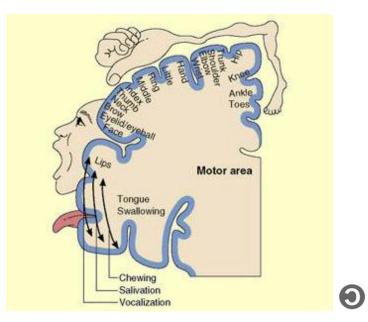


Figure 3: A Representation of Penfield's Map of the Motor homunculus. Image represents Penfield's map of the motor homunculus in a coronal view down the middle of the central sulcus, and was retrieved from McGill's website "The brain from top to bottom" (Dubac, 2002).

Previous neuroimaging research has shown evidence of somatotopic-semantic representations in the sensorimotor and premotor cortices during the processing of action-related language (Boulenger & Nazir, 2010; Hauk et al., 2004; 2008; Martin, 2007; Pulvermuller, 2005; Raposo, Moss, Stamatakis, & Tyler, 2009; Tettamanti et al., 2005). Such studies have shown activation in the sensorimotor regions that is organized somatotopically (much like Penfield's map of the sensory and motor homunculi, Penfield & Boldrey, 1937) during the processing of action-related language (Hauk et al., 2004; Tettamanti et al., 2005; Martin, 2007). Specifically, research has shown that action-related language activates the parietal-frontocentral network (PFN; consisting of the parietal, sensorimotor, premotor and frontal regions) in a somatotopic fashion dependent upon the body part the object/action represents (Hauk et al., 2004; 2008; Martin, 2007; Pulvermuller, 2005; Raposo et al., 2009; Tettamanti et al., 2005). For example, Hauk et al. (2004) had participants complete a motor localization and passive reading task. In the motor localization task, participants performed tongue, hand, and foot movements to localize each body parts' representation along the motor cortex. In the passive reading task, participants covertly read action words (e.g., lick, pick, and kick) referring to specific body parts (e.g., mouth, arm, and leg). The authors found that when participants covertly read action words

referring to specific body parts, regions proximal to where the body part is represented on the motor cortex were activated. Specifically, face words activated the bilateral inferior-frontal premotor cortex, arm words activated the bilateral premotor cortex dorsal to where face words were processed and the left precentral gyrus, while leg words activated the dorsal left precentral and postcentral gyri and premotor cortex along the midline. Moreover, Hauk and colleagues found overlap between motor movements and silent action-word reading along the motor cortex that was somatotopically organized, supporting the notion that motor regions respond to actionrelated semantic information. Tettamanti et al. (2005) found that listening to action-related sentences referring to specific body parts (e.g., mouth, arm, and leg) produced somatotopic activation in the left parietal-frontocentral and temporal cortices. In particular, participants listened to action-related sentences referring to specific body parts (e.g., "I bite an apple"; "I grasp a knife"; and "I kick the ball") and a baseline condition consisting of abstract sentences that contained no motor content (e.g., "I appreciate sincerity"). Regions of brain activation from the action-related sentences were compared to brain activation from the abstract sentences to determine whether activation of motor regions was due to the motor component of, or action representation within, the sentence. The authors found that mouth sentences activated the pars opercularis and triangularis of the inferior frontal gyrus, which is just anterior to the motor cortex for the mouth; hand sentences activated the left precentral gyrus (near where hand is represented along the motor cortex), the left posterior intraparietal sulcus, left posterior inferior temporal gyrus, left insula, and the right middle temporal gyrus; and leg sentences activated the left dorsal premotor cortex (proximal to the motor cortex for legs and dorsal to the regions the hand sentences activated) and the left inferior parietal lobule (Tettamanti et al.). In addition, Boulenger et al. (2009) found the frontocentral regions to be somatotopically organized when participants silently read idioms referring to actions of specific body parts. In particular, stronger activation was shown for arm idioms (e.g., "He grasped the idea") in the lateral motor cortex, while stronger activation was shown for leg idioms (e.g., "He kicked the habit") in the dorsal motor cortex (Boulenger et al., 2009). These results are consistent with neuroimaging studies examining cortical activation during action observation, which have shown that the observation of effector-specific (e.g., hand, mouth, and foot) actions produces somatotopic activation in the premotor cortices and posterior parietal lobe (Buccino et al., 2001).

Interestingly, Aziz-Zadeh, Wilson, Rizzolatti, and Iacoboni (2006a) found that regions in the premotor cortex activated when observing actions overlapped with regions activated when reading phrases depicting actions, and this activation was somatotopically organized. In this experiment, participants viewed actions that were performed by the mouth, hand, and foot, and also read literal and metaphorical phrases representing the mouth, hand, and foot. Activation for the action observation condition was compared to activation for the action reading condition. Region of interest (ROI) analyses demonstrated that regions activated for effector-specific action observation were also most strongly activated during the reading of the same effector-specific action, and furthermore, this was somatotopically organized (e.g., action observation and action reading for the mouth activated the ventral premotor cortex, while action observation and action reading for the hand activated a more dorsal portion of the premotor cortex). Thus, these results show that activation for effector-specific action observation overlaps with linguistic representations of effector-specific actions. This suggests that the motor and premotor cortices brought online during action observation are also engaged when retrieving conceptual information about such actions. As such, Aziz-Zadeh and colleagues proposed that these results show that the same embodied representations are active during action observation and reading action descriptions. These results provide support for the embodied perspective, whereby the understanding of an action concept requires the mental re-enactment of the action (as shown by overlap between action observation and verbal descriptions of the action).

The above mentioned results are consistent with the theory of embodied cognition, in that to understand action-related semantic information, re-enactment of the action associated with the referent must occur in the sensorimotor and premotor cortices. That is, when reading and listening to action words or sentences, the sensorimotor and premotor cortices are activated. Furthermore, this research suggests that the parietal-frontocentral network is activated in a somatotopic fashion when the language emphasizes motor processing, or in other words, is embodied.

The somatotopic-semantic activation that has been shown when participants' process action-related language has also been suggested to be evidence of a human mirror neuron system (MNS) (Hauk et al., 2004; Tettamanti et al., 2005). Mirror neurons were first discovered in the primate premotor cortex, area F5, and were found to respond to actions performed by a monkey and also during the observation of the same goal-directed actions (di Pallegrino, Fadiga, Fogassi,

Gallese, and Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Rizzolatti and Craghero, 2004). Moreover, previous neuroimaging research has shown evidence of a MNS in humans during action-observation and execution (Aziz-Zadeh, Koski, Zaidel, Mazziotta, and Iacoboni, 2006b; Fadiga, Fogassi, Pavesi, and Rizzolatti, 1995; Rizzolatti and Craighero, 2004). For example, Aziz-Zadeh et al. (2006b) showed bilateral activation of the human MNS (regions in the left and right pars opercularis of the inferior frontal gyrus and the inferior parietal lobule) when participants observed, imitated, and executed a hand action. As such, the somatotopic-semantic activation shown when participants respond to action-related semantic knowledge (Boulenger et al., 2009; Hauk et al., 2004; Tettamanti et al., 2005), and furthermore, the finding of overlapping activation during motor movements and when responding to action words (Hauk et al.), suggests that the mirror neuron system may be activated when responding to tasks targeting action-related semantic knowledge.

Rationale for My Research

As discussed above, previous research has shown that when participants covertly read or listen to action-related words or sentences, the PFN is activated in a somatotopic fashion. However, the experiments used in previous research have not directly targeted an individual's own representation of an object's use, and furthermore, have not examined whether the PFN is activated somatotopically when an individual provides their own use for an object. That is, does providing an overt response to effector-specific (arm or leg) stimuli activate the PFN in proximity (both anterior and posterior) to where hands/arms and feet/legs are represented along the sensorimotor cortices? Thus, to be able to examine how the PFN responds when an individual provides their own use for a stimulus (that is, accesses their own semantic knowledge), we developed a new semantic generation task. This requires individuals to generate a verbal response indicating how they would interact with specific objects typically used by the arm or leg. Moreover, the gapped paradigm that will be used in the fMRI experiments allows time for participants to provide a response in the MRI. As such, by using a semantic generation task and a paradigm that allows an individual to produce their own representation of how to use an object, this research will provide a more ecologically valid examination of embodied cognition. Furthermore, previous research has not directly compared differences in PFN activation when participants provide their own use for a stimulus presented in both picture and

word format. As such, a new stimulus set was developed that contains objects that can be presented in picture and word format, in an attempt to facilitate direct comparison of processing in the PFN dependent upon stimulus presentation format. In addition, the stimulus set that was developed contains objects that participants should have experience interacting with, so as to be sure that an individual's own experience and knowledge of an object's use could be provided.

In addition, the use of unique and shared maps developed in our lab (Borowsky et al., 2005a; 2005b) will allow for a more comprehensive examination of the theory of embodied cognition. For example, these shared maps allow one to determine what activation is common between two tasks, while unique activation maps allow one to determine what regions are uniquely activated for each task. This differs from the traditional examination of what is unique to each task using subtraction activation maps, whereby traditional subtraction maps show unique activation based on what task activation is more significant than the other task activation. As such, the unique and shared maps used in the fMRI analysis in the neuroanatomical experiments will allow for a better examination of what is unique to motor and semantic processing, and also, what is shared between motor and semantic processing. That is, this analysis will enable one to determine: 1) what regions of activation are unique to a motor localization task (hand and foot movements); 2) what regions of activation are unique to the semantic generation task ("how would you interact with the object?"); and 3) what regions of activation are shared between the motor localization and semantic generation tasks in the PFN. Thus, if there is unique effector-specific activation for the semantic generation task in proximity to regions activated during effector-specific movements, then this would indicate that the PFN is activated somatotopically during a semantic generation task; however, if the PFN is not activated somatotopically during a semantic generation task (i.e., no somatotopically organized effectorspecific activation in proximity to the sensorimotor cortices) then this would provide support for amodal or disembodied theories of semantic processing. Furthermore, a more precise examination of whether the motor system shows evidence of being embodied would be to examine whether there is shared activation between the motor localization and semantic generation tasks. Specifically, shared activation between a motor and semantic generation task would suggest that the motor system is involved in semantic processing, and moreover, that retrieving action-related semantic knowledge requires the recruitment of the motor system. Additionally, shared activation between the semantic generation and motor localization tasks

would provide further evidence in favour of a human mirror neuron system. However, if shared activation is not shown between these two tasks in the PFN, then this would provide support for disembodied theories that suggest that the motor system is not required during the processing of action-related semantic information.

Does the Presentation Format of a Stimulus Affect the Processing of Embodied Stimuli?

One goal of the research presented in this dissertation is to examine whether picture and word stimuli are processed in unique (separate) or shared (common) brain regions that have been shown to process embodied semantic information (e.g., parietal-frontocentral brain regions). That is, will picture and word stimuli representing objects that can be interacted with by the arm/hand or leg/foot be processed in separate brain regions (activation of modular or unique brain regions), or processed in the same brain regions (activation of common or shared brain regions)? Another goal of the research presented in this dissertation is to examine whether pictures and words have differential access to action-related semantic information. Previous research has shown that patients can present with deficits in recognition and comprehension dependent upon the presentation format of a stimulus. For example, Bub, Black, Hampson, and Kertesz (1988) identified a severe impairment in word comprehension, but intact picture comprehension, in a brain damaged patient. Similarly, Lambon Ralph and Howard (2000) describe a patient, I.W., who had progressive fluent aphasia, which is characterized by atrophy to the left inferior and lateral portions of the temporal cortex, typically resulting in semantic comprehension deficits and anomia (word finding difficulties). I.W. had poor verbal comprehension and word finding difficulties, but intact picture comprehension and knowledge about object use. Alternatively, Lhermitte and Beauvois (1973) described an optic aphasic patient, J.F., who showed no impairment in repeating words and sentences, producing the definition to words, naming objects from tactile presentation, and pantomiming an objects' use, but showed impairments in naming pictures of objects and naming objects presented visually. Such patient studies showing a dissociation between object identification and/or word reading and comprehension raises the possibility that pictures and words may be processed in fairly separate (and possibly separate) semantic systems.

Behavioural research has also shown differential processing of pictures and words, with both presentation formats being shown to have differential access to action-related semantic knowledge. Specifically, Thompson-Schill, Kan, and Oliver (2006) suggest that stimuli

presented in different presentation formats have stronger associations with distinct attribute domains, thus providing access to different types of semantic knowledge. For example, when compared to word stimuli, picture stimuli are thought to contain a greater amount of form information, which provides picture stimuli with privileged access to knowledge about object manipulation as compared to words (Thompson-Schill et al.). This notion was supported by Chainey and Humphreys (2002) who found that participants are faster at making action decisions based on picture stimuli compared to word stimuli. Chainey and Humphreys had participants name objects and words, make an action decision about an object, word, or non-object (e.g., "is pouring or twisting the more appropriate action for the object?"), and make a semantic decision about the stimulus (e.g., is the object found in the kitchen?). The authors found that participants named words faster than pictures, but showed no difference between pictures and words for semantic decisions. Furthermore, participants were faster with semantic decisions compared to action decisions for words, and were faster making action decisions for pictures compared to words. These results suggest that picture stimuli have privileged access to action knowledge, whereas word stimuli have privileged access to word-associated knowledge (e.g., orthography and phonology). As such, Chainay and Humpheys (2002) suggest that the action decision advantage found for objects occurs because stored associations for actions are easily accessed by the visual properties of the object.

Additionally, Saffran, Coslett, and Keener (2003) examined whether pictures and words show differential access to action-related semantic information by investigating whether participants produced a greater number of verb associates to picture versus word, manipulable versus non-manipulable, and animate versus inanimate, stimuli. Participants were shown pictures and words and were instructed to produce the first word that came to mind. The authors found that participants produced a significantly greater number of verbs to pictures than words, to manipulable (e.g., apple or balloon) versus non-manipulable (e.g., bride or ambulance), and to inanimate (e.g., book or bus) versus animate (e.g., baby or cow) stimuli, with the greatest number of verbs being elicited for pictures of inanimate manipulable objects (e.g., ball). As such, these results provide further support for the notion that pictures and words have access to different attributes or representations (Thompson-Schill et al., 2006). Saffran et al. suggest that the greater proportion of verbs being produced for picture compared to word stimuli occurs because pictures provide the affordance of how the object can be used, thus making it easier to produce a verb

representing the object's use. Furthermore, Caramazza et al. (1990) suggest that objects (or pictures of objects) have direct associations with meaning, whereas words do not. As such, Saffran and colleagues propose that these associations between pictures and meaning, compared to words and meaning, may be why a greater proportion of verbs are produced when the target stimuli are pictures compared words. Thus, together these results suggest that although both pictures and words have access to common action-related semantic knowledge (given that verbs are produced for both pictures and words), there are differences in the amount of action-related semantic knowledge accessible dependent upon whether this information is presented in picture or word format.

Finally, given that patient and behavioural studies have shown that pictures and words have differential access to semantic representations, neuroimaging research has sought to examine whether pictures and words are processed in unique (separate) or shared (common) brain regions. Previous neuroimaging research has shown evidence of both unique and shared activation during the processing of picture and word stimuli (Borowsky et al., 2005a; Borowsky, Esopenko, Cummine, & Sarty, 2007; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). For example, research by Vandenberghe et al., (1996), has shown a network of shared activation for pictures and words, as well as regions where activation was significantly greater for pictures compared to words. Specifically, Vandenberghe and colleagues used PET to examine the processing of pictures and words in two semantic tasks targeting associative semantic knowledge and visual semantics, and a baseline task that involved matching stimuli based on physical size. For the semantic tasks the authors found unique activation for pictures in the left posterior inferior sulcus; unique semantic activation for words in the left superior temporal sulcus, left anterior middle temporal gyrus, and left inferior frontal sulcus; and finally, a network of common activation for pictures and words extending from the left superior occipital gyrus to the middle and inferior temporal cortex to the inferior frontal gyrus. Furthermore, previous research from our laboratory has also shown neuroimaging evidence in favour of unique and shared processing for picture and word stimuli (Borowsky et al., 2005a). For example, Borowsky et al. (2005a) examined the processing of picture and word stimuli in the "what" (i.e., ventral), "where" (i.e., dorsal), and "how" (i.e., mid-dorsal) processing streams. In the "what" task participants named picture and word stimuli, in the "where" task participants produced the cardinal location of the stimulus, and in the "how" task participants stated how they would interact with the picture or

word. Borowsky and colleagues found that there were unique and shared regions of activation in the "what" and "where" streams for pictures and words, and importantly for the research carried out in this dissertation, unique and shared activation in the "how" stream for picture and word stimuli. Specifically, in the "how" task, shared activation for pictures and words was found in the left middle dorsal stream, including the supramarginal gyrus, ventral motor cortex, and bilateral medial and lateral superior frontal gyrus; activation unique to picture stimuli was found in the dorsal stream including the right superior parietal lobule and angular gyrus, left superior frontal and inferior frontal gyri, left ventral motor cortex, and right medial frontal cortex; and finally, unique activation for word stimuli was found in the middle dorsal stream including the bilateral angular gyrus, superior parietal lobule, and superior motor cortex, left superior and middle frontal gyri, and left medial occipital to frontal gyri. As such, these results suggest that pictures and words are processed in both unique (modular) and shared (common) brain regions. Furthermore, the research by Borowsky and colleagues suggests that there is shared and unique activation for pictures and words in regions that process action-related semantic information.

Taken together the aforementioned results suggest that there are not only overlapping action-semantic representations between picture and word stimuli, but also that pictures and words have differential access to action-semantic systems. However, previous studies have not examined whether there are differences in the processing of action-related semantic information dependent upon presentation format (e.g., pictures and words) using stimuli that target effector-specific actions (e.g., arm or leg). As such, the research in this dissertation involves examining how presentation format affects the processing of action-related stimuli in the parietal-frontocentral networks.

Conclusion

Previous neuroimaging and behavioural research have provided support for the theory of embodied cognition. However, previous research has not examined the processing of actionrelated stimuli by having an individual provide their own use, or action-related semantic representation, for a stimulus, nor has previous research compared the processing of the same stimuli and tasks using different experimental paradigms (fMRI, behavioural, and patient), or between presentation formats (e.g., pictures and words). The semantic generation task requires individuals to generate a response to how they would interact with an object typically used by the arm or leg. By using a semantic generation task that targets an individual's own representation of

how they use an object, this research provides a more ecologically valid examination of embodied cognition and somatotopic-semantic representations. In addition, the same objects are presented in picture and word format, so as to be able to directly compare whether there were differences in access to action-related semantic representations dependent upon the presentation format of the stimulus. Finally, building on the first stimulus set, additional word stimuli were developed and BOI ratings were collected, to examine how the processing of arm and leg stimuli is affected in a task that requires participants to respond with either their hand or foot. BOI ratings were collected on this stimulus set to examine whether arm and leg words rated as higher in BOI were responded to more quickly than words rated as lower in BOI when responding with the hand or foot. Additionally, whether the relationship between reaction times and accuracy with BOI is affected by the congruence and dominance of the response effector was examined.

To provide a comprehensive examination of embodied cognition, Chapter 2 examines how action-related word stimuli are processed in the sensorimotor and premotor cortices. Chapter 3 replicates and expands on the results from Chapter 2, and moreover, examines how action-related picture stimuli are processed in the PFN. Chapter 3 will also examine whether pictures and words are processed in shared or unique regions in the PFN, and whether there are shared regions of activation between a motor localization task and the semantic generation tasks. Chapter 4 will examine whether there are differences in the processing of arm and leg picture and word stimuli in a naming and semantic generation task in both healthy controls and in an individual post-right and an individual post-left hemispherectomy. Moreover, Chapter 4 will evaluate the necessity versus sufficiency of the right and left hemispheres for processing these tasks and stimuli. For example, according to Price, Noppeney, and Friston (2006), neuroimaging research on normal individuals can show us what regions may be sufficient (i.e., may be involved) for a specific task or function. However, Price and colleagues further suggest that the only way to determine whether a brain region is *necessary* to perform a given task or function is through a lesion to the brain region that results in a deficit in performing the task, or in other words, when performance falls well outside normal levels of performance. As such, comparing the processing of healthy controls to individuals post-hemispherectomy will help to determine which regions are sufficient to complete the naming and semantic generation tasks, and which regions are necessary to carry-out these tasks. Chapter 5 will provide an examination of whether there is a BOI advantage shown for arm and leg words rated as higher in BOI, and whether the

congruence and dominance of the response effector affects the relationship between reaction times and accuracy with BOI. Furthermore, Chapter 5 will examine how the congruence and dominance of the effector response (e.g., responding with the dominant or non-dominant hand and foot) affects responding in a semantic categorization task.

CHAPTER 2

AN EXAMINATION OF THE PROCESSING OF ACTION-RELATED WORD STIMULI IN THE PREMOTOR AND SENSORIMOTOR CORTICES

Portions of this chapter has been previously published:

Esopenko, C. Borowsky R. Cummine J. & Sarty G. (2008). Mapping the semantic homunculus: A functional and behavioural analysis of overt semantic generation. *Brain Topography*, 22(1), 22-35, doi: 10.1007/s10548-008-0043-8

As described in detail in Chapter 1, embodied cognition theorists postulate that the interaction between the body and environment shapes conceptual processing, whereby conceptual processing is grounded in sensorimotor experiences (Barsalou, 1999; Gibbs, 2006; Siakaluk et al., 2008a; 2008b; Wilson, 2002). Furthermore, it has been suggested that the retrieval of conceptual representations requires the simulation of sensorimotor experiences through the recruitment of the sensorimotor and premotor cortices (Barsalou, 1999; 2008b; Gallese & Lakoff, 2005). As such, one goal of research examining the theory of embodied cognition is to determine whether the processing of action-related semantic information activates the sensorimotor and premotor cortices. Previous neuroimaging research has shown that presenting participants with action-related stimuli activates the sensorimotor and premotor cortices (Boulenger et al., 2009; Hauk et al., 2004; 2008; Martin, 2007; Pulvermuller, 2005; Tettamanti et al., 2005). However, it remained to be determined whether the sensorimotor and premotor cortices are activated when an individual has to provide their own use, or action-related semantic knowledge, for a stimulus.

The first goal of Experiment 1 was to determine whether the sensorimotor and premotor regions are activated when responding to a word-based semantic generation task and whether this activation is somatotopically organized. That is, does an arm- and leg-based word semantic generation task activate the sensorimotor and premotor regions proximal to where the body part is represented along the sensorimotor cortices based on Penfield's map of the sensory and motor homunculi (Penfield & Boldrey, 1937)? A second goal of Experiment 1 was to determine whether there would be shared, or common, activation between the semantic generation and

motor localization tasks. Evidence of shared activation between the motor localization and semantic generation tasks would provide support for the theory of embodied cognition, in that shared activation between a motor localization and semantic generation task would imply that the same regions that are responsible for motor processing also process action-related semantic information. To examine this question, participants completed: (1) a motor localization task, where they were required to move either their hands or feet, and (2) a word semantic generation task, where they were required to generate their own responses as to how they would interact with an object that was associated with either their arm/hand or leg/foot, as part of a fMRI study. Patterns of brain activation were examined to determine whether the semantic generation task produced a somatotopic pattern of activation in the sensorimotor and premotor cortices.

Experiment 1

Materials and Methods

Participants

University graduate students (N = 8; mean age = 25) with normal or corrected to normal vision participated in Experiment 1. Four participants completed the arm version of the motor localization and semantic generation tasks, and four participants completed the leg version of the motor localization and semantic generation tasks. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences and Biomedical Sciences Ethics Committees.

Stimuli and Procedure

In Experiment 1, participants completed a motor localization task and a word semantic generation task. Participants completed the motor localization task to determine the location of hand and foot representations along the motor cortex. To allow comparisons to the tasks described below, a visual cue was given on each trial, such that in the arm condition the word "Hand", and in the leg condition the word "Foot", was presented on the screen and participants were instructed to move the body parts that the word represented while it was on the screen. For the arm motor task, movement involved bimanual sequential finger-to-thumb movements. For the leg motor task, movement involved bimanual foot-pedaling motions. For the foot-pedaling motions, participants were instructed to only move their feet and no other part of their body. Using a large-angled piece of foam under the knees in the foot-pedaling condition made it so that there was no motion in the upper body.

For the semantic generation task, the stimuli consisted of words referring to objects that are typically used by the arm/hand (e.g., stapler) or the leg/foot (e.g., soccerball). There were 50 objects in word task (25 arm stimuli and 25 leg stimuli; see Appendix A for a complete list of stimuli). Participants were presented with blocks of words (with 5 words in each block) referring to objects that are primarily used by either the arm/hand or the leg/foot and were instructed to quickly describe how they would physically interact with the object. This paradigm allows the participant to apply their own conceptual knowledge about the objects. Participants were instructed to give responses during a gap in image acquisition (see below). This allowed the experimenter to listen to each response to ensure that the participant provided a response that was appropriate for the task (Borowsky et al., 2005a; Borowsky et al., 2007). Examples of arm

responses included "write" or "hold it", while examples of leg responses included "kick", "wear it" or "jump on it". The semantic generation task always followed the motor localization task, so that no effects from the more complex semantic generation tasks carried over into the simpler motor task.

Imaging and Image Analysis

The imaging was conducted using a 1.5T Siemens Symphony (Erlanger, Germany) magnetic resonance imager. For both the motor and semantic generation tasks, 55 image volumes were obtained, with each image volume consisting of 12 axial slice single-shot fatsaturated echo-planar images (EPI); $T_R=3300$ ms, with a 1650 ms gap of no image acquisition at the end of the T_R, T_E=55 ms, 64×64 acquisition matrix, 128×128 reconstruction matrix. Each slice was 8mm thick with a 2mm thick interslice gap and was acquired in an interleaved sequence (e.g., slices 1-3-5-2-4 etc.) to reduce partial volume crosstalk in the slice dimension. For all tasks, the first 5 image volumes were used to achieve a steady state and were discarded prior to analysis. The remaining volumes were organized into 5 blocks of 10 volumes each for a total of 50 image volumes. Each block consisted of 5 image volumes collected during the presentation of, and responses to, the stimuli, followed by 5 image volumes collected during rest. A computer running EPrime software (Psychology Software Tools, Inc., Pittsburgh, PA) was used to trigger each image acquisition in synchrony with the presentation of visual stimuli. The stimuli were presented using a data projector (interfaced with the Eprime computer) and a backprojection screen that was visible to the participant through a mirror attached to the head coil. In order to capture a full-cortex volume of images for each participant, either the third or fourth inferior-most slice was centered on the posterior commissure, depending on the superior-inferior distance between the posterior commissure and the top of the brain for each participant. T₁weighted high-resolution spin-echo anatomical images (T_R = 400ms, T_E = 12 ms, 256 × 256 acquisition matrix, 8 mm slice thickness with 2 mm between slices) were acquired in axial, sagittal, and coronal planes for the purpose of overlaying the activation maps. The position of the twelve T₁ axial images matched the echo-planar images; nineteen slices each were obtained in the sagittal and coronal orientations.

The motor localization and semantic generation tasks were analyzed using the BOLDfold technique, which is a well established technique in our lab that involves correlating the raw data with the averaged blood oxygen level dependent (BOLD) function (Sarty & Borowsky, 2005).

This method of analysis requires that sufficient time elapse between blocks for the hemodynamic response function (HRF or BOLD function) to fully return to baseline levels. After correcting for baseline drift, the mean BOLD function for each voxel, collapsing across the repetitions of task and baseline, was empirically determined with the BOLDfold method (which is a general linear model [GLM] parametrization of the HRF) and then repeated and correlated to the actual data as a measure of consistency across repetitions. In other words, the empirically determined BOLD function was correlated to the actual data as a measure of consistency across repetitions. The squared correlation (r^2) represents the goodness of fit between the mean BOLD function and the observed BOLD data, capturing the variance accounted for in the data by the mean BOLD response. This method also serves to reduce the number of false activations associated with the traditional t test method, and, in particular, it is less sensitive to motion artifacts (Sarty & Borowsky, 2005). The correlation, r, was used as follows. A threshold correlation of r = 0.60was used to define an active voxel. The false-positive probability is p < .05 with this threshold serving as a Bonferroni-correction for 100,000 comparisons (the approximate number of voxels in an image volume). The use of both a gap in image acquisition and the BOLDfold analysis method minimizes motion artifact (Sarty & Borowsky, 2005) and has been used successfully several times. (e.g., Borowsky, Owen, & Sarty, 2002; Borowsky et al., 2005a; Borowsky et al., 2005b; Borowsky, et al., 2006; Borowsky et al., 2007; Cummine, Borowsky, & Sarty, 2010; Cummine, Borowsky, Vakorin, Bird, & Sarty, 2008; Farthing, Borowsky, Chillibeck, Binsted, & Sarty, 2007; Farthing, Cummine, Borowsky, Chilibeck, Binsted, & Sarty, 2007; Hall et al., 2008; Owen, Borowsky & Sarty, 2004; Vakorin, Borowsky, & Sarty, 2007).

FMRI maps were computed for the motor localization and semantic generation tasks using a technique for separating activations unique to each condition from those that are shared between conditions (Borowsky et al., 2005a). For each condition, C, for each participant, a threshold map $r_{\rm C}(p)$ of *r* correlation values and a visibility map $V_{\rm C}(p)$ (intensity of BOLD amplitude) were computed where p is a voxel coordinate. The corresponding activation map for C, for each participant, was defined as $M_{\rm C}(p) = \chi_{\rm C,\theta}(p) V_{\rm C}(p)$ where $\chi_{\rm C,\theta}(p) = 1$ if $r_{\rm C}(p) > \theta$ and zero otherwise. We used a threshold of $\theta = 0.60$ to define active voxels. The threshold value represents a minimal acceptable correlation between the measured BOLD response and its blocked mean repeated across the five blocks before a voxel is declared active. Intersection maps (M_{int}) , and unique maps (M_{uni}) were computed for paired conditions A and B for each participant according to:

$$M_{uni}(p) = [\chi_{A,\theta}(p) V_A(p) - \chi_{B,\theta}(p) V_B(p)] [1 - \chi_{A,\theta}(p) \chi_{B,\theta}(p)]$$
(1)

$$M_{int}(p) = \chi_{A,\theta}(p) \chi_{B,\theta}(p) (V_A(p) + V_B(p))/2$$
(2)

The unique map represents a difference $(A \cup B) \setminus (A \cap B)$ and shows task subtraction for activations that are not common to conditions A and B (A is > 0, B is < 0). The intersection map represents an intersection A \cap B showing activation common to both conditions A and B with the activation amplitude coded as the average of A and B. Unique and intersection maps were averaged across participants separately for each condition after smoothing and transformation to Talairach coordinates (Talairach & Tournoux, 1988) to produce the final maps as described below.

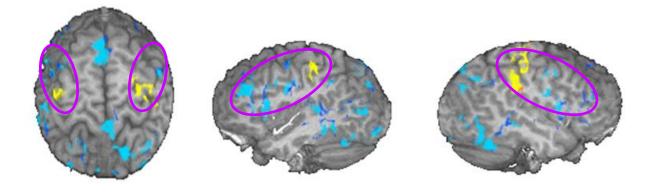
Using the AFNI software (Cox, 1996), voxels separated by 1.1 mm distance (i.e., the effective inplane voxel resolution) were clustered, and clusters of volume less than 100 µL were clipped out at the participant level. The data were then spatially blurred using an isotropic Gaussian blur with a full width at half maximum (FWHM) of 3.91 mm (2 pixels). The averaging of images across subjects was subsequently done after Talairach transformation to a standardized brain atlas (Talairach & Tournoux, 1988). Visual inspection of the individual participant anatomical images did not reveal any structural abnormalities that would compromise the averaging of data in Talairach space. Mean activation maps in Talairach coordinates were determined for each map type along with the corresponding one sample *t* statistic for map amplitude for each voxel. The final maps for the motor localization and semantic generation tasks surpass the θ threshold at an individual level, and a one-tailed *t* test of map amplitude against zero at the group level. Regions of activation on the resulting maps were deemed significant for each of the arm and leg conditions at *t*(3) = 2.353, *p*<.05.

Results

Regions activated during the motor localization and semantic generation tasks are shown and described in Figures 4 and 5. Figure 4a shows unique regions of activation for the arm motor localization and semantic generation task, while Figure 4b shows shared regions of activation between the arm motor localization and semantic generation task. Figure 5a shows unique regions of activation for the leg motor localization and semantic generation task, while Figure 5b shows shared regions of activation between the leg motor localization and semantic generation task. The results show somatotopic-semantic activation for both arm and leg stimuli, whereby the semantic generation tasks produced activation proximal to where each body part is represented along the motor cortex. Somatotopically organized shared activation was only found for arm stimuli.

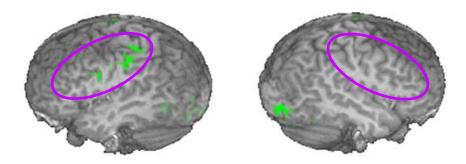
Figure 4. Arm (a) Unique and (b) Shared Activation for the Motor Localization and Semantic Generation Task in the Sensorimotor and Premotor Regions (area included in the ellipses)

(a) Unique activation



Activation was found for the motor localization task (yellow coded activation) in the precentral gyrus where the arm is represented on the motor homunculus (Penfield and Boldrey, 1937). Unique activation for the arm semantic generation task (blue coded activation) was found in the premotor cortex, middle frontal gyrus (MFG), and inferior frontal gurus (IFG) in both the left and right hemispheres in the premotor cortex directly anterior to where arm is represented on the motor homunculus. Regions of activation outside the premotor and sensorimotor cortices for the arm semantic generation task was found in the bilateral middle temporal gyrus (MTG), lateral occipital gyrus (LOG), and superior parietal lobule (SPL), and left angular gyrus (AG).

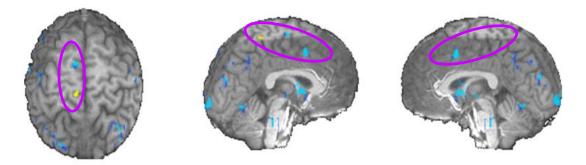
(b) Shared Activation



The shared maps for the arm motor localization and semantic generation tasks indicate that there is shared activation (green coded activation) in precentral gyrus, SPL, MFG, and IFG in the left hemisphere. Regions of shared activation outside the premotor and sensorimotor cortices were found in the bilateral LOG and left MTG.

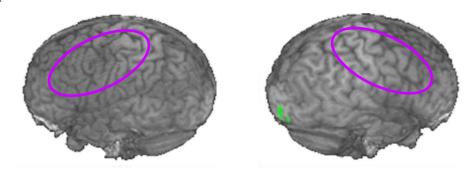
Figure 5. Leg (a) Unique and (b) Shared Activation for the Motor Localization and Semantic Generation Task in the Sensorimotor and Premotor Regions (area included in the ellipses)

(a) Unique activation



Activation was found for the motor localization task (yellow coded activation) on the left precentral gyrus (motor cortex) where leg is represented on the motor homunculus (Penfield and Boldrey, 1937). For the leg semantic generation task (blue coded activation), activation was found directly anterior to motor localization task activation in the left supplementary motor area (SMA), and the bilateral superior frontal gyrus (SFG). Unique activation for the leg semantic generation task outside the premotor and sensorimotor cortices was found in the bilateral SPL, thalamus, precuneus, cuneus, and cerebellum.

b) Shared activation



The shared maps for the motor localization and semantic generation to leg word stimuli indicate that there is shared activation (green coded activation) in the occipital cortex of the right hemisphere.

Discussion

The results provide evidence that the premotor cortex is involved in the retrieval of action-related semantic information. Activation in the motor localization tasks was found along the motor cortex, which is in accordance to Penfield's Map of the motor homunculus (Penfield & Boldrey, 1937). Unique activation in the semantic generation task (i.e., for both arm and leg) was found directly anterior to the motor cortex (precentral gyrus) and was somatotopically organized. The findings from the semantic generation task parallel those from previous research, whereby activation was found in the premotor cortex during the processing of action-related stimuli (Hauk et al., 2004; Pulvermuller, 2005; Tettamanti et al., 2005). As such, the results from Experiment 1 show that when participants are required to generate their own use, or action-related semantic representation, to a word referring to an object used by the arm or leg, activation patterns were similar to those seen in previous studies that examined silent reading of action-words or listening to action-related sentences. Furthermore, these findings are consistent with the theory of embodied cognition whereby conceptual knowledge is grounded in sensorimotor experiences, and that it is retrieved through activation of those same sensorimotor regions (Barsalou, 1999). Taken together, these findings provide support for the somatotopic-semantic organization of the premotor cortices during tasks that target action-related semantic knowledge.

A second goal of this research was to examine whether there was shared activation between the semantic generation and motor localization tasks, as this would provide further evidence in favour of the theory of embodied cognition. Specifically, if shared activation was found between a motor task and a semantic task, then this would show that the motor regions also process semantic information. Furthermore, if shared activation was found between these two tasks, then this would provide support for the idea that when retrieving semantic information, the perceptual, or sensorimotor, experiences that occurred when encoding such information are simulated. Shared activation was found for arm stimuli between the semantic generation and motor localization tasks and was organized somatotopically, whereby shared activation for arm stimuli was located in the lateral frontocentral cortex. Thus for arm stimuli, the results provide evidence consistent with the embodied cognition framework, whereby regions that are responsible for motor movements of the arm are also accessed when retrieving actionrelated semantic information about the arm. However, for leg stimuli, shared activation was only found in the lateral occipital gyrus (LOG). The lack of shared activation for leg stimuli could be

due to two reasons. The first being that since visual inspection of the activation maps shows less activation overall for leg stimuli, the lack of shared activation between the motor localization and semantic generation tasks in the sensorimotor regions may be due to the small sample size in this study. That is, with an increased sample size, there may be more power to pick up shared activation for leg stimuli.

The second explanation as to why shared activation between the leg semantic generation and motor localization tasks was only found in the LOG could be due to differences in the complexity of motor programs associated with arm and legs. Specifically, Pulvermuller, Hauk, Nikulin, and Ilmoniemi (2005a) found that when TMS was applied to areas of the motor cortex that represents specific body parts, there were no differences in response times for arm words regardless of whether TMS was applied to the arm region of the motor cortex, or to the leg region of the motor cortex. However, when stimulation was applied to the area of the motor cortex where the leg is represented, leg action words were responded to faster than when stimulation was applied to the arm site (Pullvermuller et al., 2005a). Pulvermuller and colleagues suggest that this may be due to leg words having a stronger reliance on their "semantic actionrelated features" compared to arm words. That is, since arm actions are more varied (Pulvermuller et al.), and people interact with objects more with their arms than their legs, they have a larger repertoire of action programs for arm. In addition, arms have a larger representation on the motor cortex than legs. Moreover, since actions associated with legs are quite stereotypical (Pulvermuller et al.) and have a less complex motor program (e.g., less dexterity or complexity is needed for walking versus writing with a pen), there is less semantic knowledge associated with those actions, thus resulting in no shared activation for the motor localization and semantic generation tasks in the premotor and motor areas for leg stimuli. As such, it could be suggested that the more complex motor programs and representation for arms in the cortex leads to increased activation in tasks involving arm stimuli. Hence, one can claim that for arms, the sensorimotor regions that are active during the actual action of a body part are also active when retrieving action-related semantic knowledge of how to interact with objects that are used by the arm (e.g., turning a door knob). An examination of whether this lack of shared activation was due to the small sample size or to the decreased extensiveness of action-related motor programs of legs will be addressed in Chapter 3.

Conclusion

The results from Chapter 2 show that the premotor cortex is activated during a semantic generation task. Specifically, the semantic generation task produced activation directly anterior and posterior to the motor cortex, and this activation was somatotopically organized dependent upon the body part the stimulus was used by. Furthermore, shared activation was found between the motor localization and semantic generation tasks in the sensorimotor and premotor regions for arm stimuli. The research carried out in Chapter 3 will extend these results to examine if the same patterns of results are shown with the inclusion of more participants, and if there are differences in the processing of action-related stimuli dependent upon the presentation format (words versus pictures) of the stimulus.

CHAPTER 3

THE EFFECT OF PRESENTATION FORMAT ON THE PROCESSING OF ACTION-RELATED STIMULI IN THE PARIETAL-FRONTOCENTRAL BRAIN REGIONS

As has been discussed, neuroimaging research has shown evidence of somatotopicsemantic representations during the processing of action-related stimuli in the PFN (Hauk et al., 2004; Pulvermuller, 2005; Raposo et al., 2009; Tettamanti et al., 2005). Moreover, such research has shown overlapping somatotopic activation between action observation and reading phrases depicting actions (Aziz-Zadeh et al., 2006a). In addition, recent neuroimaging research has found evidence of both unique and shared activation during the processing of picture and word stimuli (e.g., Borowsky et al., 2005; Vandenberghe et al., 1996). However, previous research has not examined how the presentation format of a stimulus affects the processing of action-related knowledge in the PFN. Specifically, previous research has not examined whether, like words, there is shared activation between a motor localization and picture semantic generation task. Furthermore, research has not yet examined whether pictures and words are processed in unique or shared regions that process action-related semantic information.

Summary and Hypotheses

Chapter 3 sought to first replicate and extend the results of Chapter 2. That is, to examine whether the semantic generation to word stimuli shows evidence of somatotopic-semantic activation more broadly throughout the PFN, in experiments with additional power as a function of doubling the number of participants; and furthermore, to determine whether differences between shared activation for arm and leg stimuli in Chapter 2 was due to differences in action programs for arms and legs, or rather due to a lack of power. The second goal of Chapter 3 was to examine whether there were differences in the processing of action-related semantic knowledge in the PFN dependent upon stimulus format (pictures versus words), and moreover, to determine whether there is also shared activation between the picture semantic generation and motor localization tasks in the PFN. As such, these experiments will compare activation patterns during a word semantic generation task, a picture semantic generation task, and a motor localization task to examine the veracity of the following hypotheses: 1) Given that previous research on somatotopic-semantics has shown that the PFN is activated regardless of presentation format in terms of whether participants read action words or listen to action-related

sentences (e.g., Hauk et al., 2004; Tettamanti et al., 2005), the semantic generation tasks will similarly activate the PFN regardless of presentation format in terms of generating responses to pictures or words; 2) Embodied cognition theorists (e.g., Barsalou, 2008a; Gallese & Lakoff, 2005) predict that the same regions are involved in both the actual production of motor movements and semantic access to the knowledge of how one interacts with objects, and thus there will be shared activation between the semantic generation and motor localization tasks in the sensorimotor and premotor regions, regardless of presentation format of the stimulus; and 3) Based on previous research (e.g., Borowsky et al., 2005; Bub et al., 1988; Lambon Ralph & Howard, 2000; Lhermitte & Beauvois, 1973), it was predicted that given that that pictures and words have been shown to be processed in unique and shared brain regions, and that patients show a dissociation between the processing of pictures and words, pictures and words should show shared and unique regions of activation in the PFN.

Experiment 2

Experiment 2 examined the processing of arm-related picture and word stimuli in the PFN during a semantic generation task.

Materials and Methods

Participants

University undergraduate and graduate students (N = 8; mean age = 23) with normal or corrected to normal vision participated in the following experiment. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences and Biomedical Sciences Ethics Committee.

Stimuli and Procedure

In the following experiment, participants completed a motor localization task, a picture semantic generation task, and a word semantic generation task. Participants completed the motor localization task to determine the location of hand representations along the motor cortex. The procedure was identical to Experiment 1, with the exception that participants moved their hand during both the gap and image acquisition as a way to increase the amount of motor activation produced by simple hand movements. This was done to provide a stronger comparison between the semantic generation and motor localization tasks.

For the semantic generation tasks, the stimuli consisted of visual cues that were presented in picture and word format referring to objects that are typically used by the arm/hand (e.g., stapler). There were 25 objects in each of the picture and word conditions (see Appendix A for a complete list of objects). Participants completed both the picture and word semantic generation tasks with arm/hand stimuli, and the same objects were presented in picture and word format. Presentation format (picture/word) was counterbalanced across participants. Pictures or words (with 5 words/pictures in each block) were presented and participants were instructed to quickly describe how they would physically interact with the object. Like Experiment 1, this paradigm allowed the participant to apply their own action-related semantic representations in response to the objects. Participants were instructed to give responses during a gap in image acquisition. This allowed the experimenter to listen to each response to ensure that the participant provided a response that was appropriate for the task (Borowsky et al., 2005; Borowsky et al., 2007). Examples of arm responses included "hold it" or "write with it". The semantic generation tasks

always followed the motor localization task; however, due to a technical error, one participant had to complete the motor localization task following the semantic generation tasks.

Imaging and Image Analysis

The same imaging and analysis methods discussed in Experiment 1 were used in Experiment 2, with the exception that regions of activation on the resulting maps were deemed significant for arm/hand stimuli at, t (7) = 1.895, p=.05, one-tailed, as a function of the additional participants, degrees of freedom, and stronger motor activation.

Results

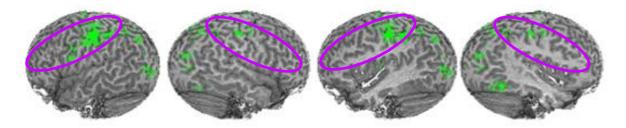
Regions of activation for the motor localization and the picture and word semantic generation tasks are shown and described in Figures 6-8. Figure 6a shows shared regions of activation between the arm motor localization and picture semantic generation tasks, while Figure 6b shows unique regions of activation for the arm motor localization and picture semantic generation tasks. Figure 7a shows shared regions of activation between the arm motor localization and word semantic generation tasks, while Figure 7b shows unique regions of activation for the arm motor localization tasks. Finally, Figure 8a shows shared regions of activation between the arm motor tasks, while Figure 8b shows unique regions of activation for the arm picture and word semantic generation tasks, while Figure 8b shows unique regions of activation for the arm picture and word semantic generation tasks.

Discussion

The results show that responding to both the arm picture and word semantic generation tasks activated the PFN somatotopically. That is, both the picture and word semantic generation tasks activated regions proximal to where arm/hand is located along the motor cortex (Figures 6b and 7b). Furthermore, an examination of the shared activation for the motor localization and arm semantic generation tasks showed shared activation that was somatotopically organized in the PFN (Figures 6a and 7a). Finally, a comparison of the arm picture and word semantic generation tasks showed both unique and shared activation for pictures and words (Figure 8).

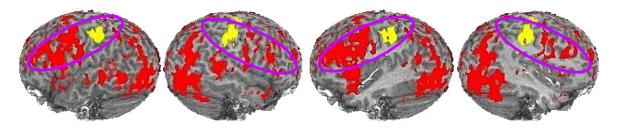
Figure 6: Arm (a) Shared and (b) Unique Activation for the Motor Localization and Picture Semantic Generation Tasks (area included in the ellipses)

(a) Shared activation



Shared activation between the motor localization and semantic generation to arm picture stimuli (green coded activation) was found in the left MFG, IFG, AG, precentral gyrus, postcentral gyrus, and SPL, and the right precentral gyrus, postcentral gyrus, and SPL. Regions of shared activation between the motor localization and semantic generation to arm picture stimuli outside the parietal-frontocentral network were found in the bilateral LOG and inferior temporal gyrus (ITG) in the right hemisphere.

(b) Unique activation

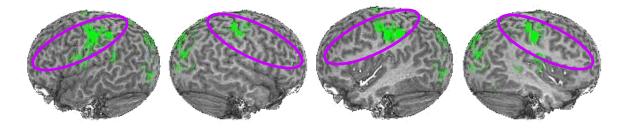


Activation unique to the motor localization task (yellow coded activation) was found in the left and right precentral and postcentral gyri, and central sulcus. For the semantic generation to arm picture stimuli (red coded activation), activation was found in the left MFG, SFG, IFG, precentral gyrus, postcentral gyrus, AG, SPL, and in the right MFG, SFG, IFG, SPL, AG, and supramarginal gyrus (SG).

Regions of unique activation outside the parietal-frontocentral network for the semantic generation to arm picture stimuli were found in the superior temporal gyrus (STG), MTG, ITG, LOG, and occipital-temporal junction in the left hemisphere, and the anterior temporal lobe, MTG, STG, temporal-occipital junction, and cerebellum in the right hemisphere.

Figure 7: Arm (a) Shared and (b) Unique Activation for the Motor Localization and Word Semantic Generation Tasks (area included in the ellipses)

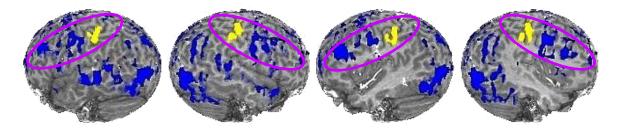
(a) Shared activation



Shared activation between the motor localization and semantic generation to arm word stimuli (green coded activation) was found in the left IFG pars opercularis, precentral gyrus, postcentral gyrus, and SPL, and the right IFG pars opercularis, precentral gyrus, and SPL.

Regions of shared activation between the motor localization task and semantic generation to words outside the parietal-frontocentral network were found in the bilateral LOG, and right MTG.

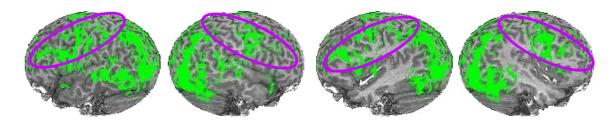
(b) Unique activation



Activation unique to the motor localization task (yellow coded activation) was found in the left precentral gyrus, postcentral gyrus, and central sulcus, and the right precentral gyrus, postcentral gyrus, and central sulcus. For the semantic generation to arm word stimuli (blue coded activation), activation was found in the left MFG, SFG, IFG pars triangularis, SPL, and AG, and the right MFG, SFG, IFG pars triangularis, precentral gyrus, SPL, and AG.

Regions of unique activation for the semantic generation to arm word stimuli outside the parietalfrontocentral network were found in the left STG, MTG, LOG, and the right anterior temporal lobe, MTG, STG, occipital-temporal junction, and cerebellum in the right hemisphere. Figure 8: Arm (a) Shared and (b) Unique Activation for the Picture and Word Semantic Generation Tasks (area included in the ellipses)

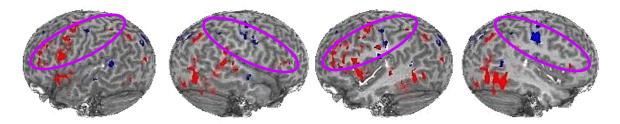
(a) Shared activation



Shared activation between the semantic generation to arm picture stimuli and arm word stimuli (green coded activation) was found in the left MFG, IFG, SFG, precentral gyrus, postcentral gyrus, SPL, and SG, and the right MFG, IFG, SFG, precentral gyrus, postcentral gyrus, SPL, and AG.

Regions of shared activation for the semantic generation to arm picture and arm word stimuli outside the parietal-frontocentral network were found in the bilateral anterior temporal lobe, STG, MTG, ITG, and LOG.

(b) Unique activation



For the semantic generation to arm picture stimuli (red coded activation), activation was found in the left SFG, MFG, IFG pars opercularis, IFG pars triangularis, precentral gyrus, and SPL, and the right AG and IFG pars orbitalis. For the semantic generation to arm word stimuli (blue coded activation), activation was found in the left precentral gyrus, and SPL, and the right precentral gyrus and SPL.

Regions of unique activation for the semantic generation to arm picture stimuli outside the parietalfrontocentral network were found in the bilateral ITG, STG, and LOG, and the right cerebellum. Regions of unique activation for the semantic generation to arm word stimuli outside the parietal-frontocentral network were found in the left STG, and the right MTG.

Experiment 3

Experiment 3 examined the processing of leg-related picture and word stimuli in the PFN during a semantic generation task.

Materials and Methods

Participants

University undergraduate and graduate students (N = 8; mean age = 23) with normal or corrected to normal vision participated in the following experiment. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences and Biomedical Sciences Ethics Committee.

Stimuli and Procedure

In the following experiment, participants completed a motor localization task, a picture semantic generation task, and a word semantic generation task. Participants completed the motor localization task to determine the location of foot representations along the motor cortex. The procedure was identical to Experiment 1, with the exception that participants moved their foot during both the gap and image acquisition as a way to increase the amount of motor activation produced by simple foot movements. This was done to provide a stronger comparison between the semantic generation and motor localization tasks.

For the semantic generation tasks, the stimuli consisted of visual cues that were pictures and words referring to objects that are typically used by the leg/foot (e.g., soccerball). There were 25 objects in each of the picture and word conditions (see Appendix A for a complete list of objects). The procedure was the same as that described in Experiment 3, however participants responded to picture and word stimuli referring to objects used by the leg/foot. Examples of leg responses included "kick it" or "jump on it".

Imaging and Image Analysis

The same imaging and analysis methods discussed in Chapter 2 were used in Experiment 3, with the exception that regions of activation on the resulting maps were deemed significant for leg/foot stimuli at, t (7) = 1.895, p=.05, one-tailed, as a function of the additional participants, degrees of freedom, and stronger motor activation.

Results

Regions of activation for the motor localization and the picture and word semantic generation tasks are shown and described in Figures 9-11. Figure 9a shows shared regions of

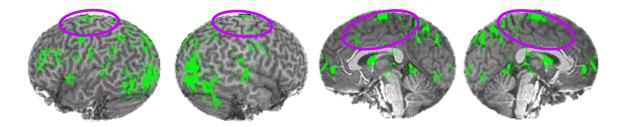
activation between the leg motor localization and picture semantic generation tasks, while Figure 9b shows unique regions of activation for the leg motor localization and picture semantic generation tasks. Figure 10a shows shared regions of activation between the leg motor localization and word semantic generation tasks, while Figure 10b shows unique regions of activation for the leg motor localization and word semantic generation tasks. Finally, 11a shows shared regions of activation between the leg picture and word semantic generation tasks, while Figure 11b shows unique regions of activation for the leg picture and word semantic generation tasks.

Discussion

The results show that responding to the leg semantic generation tasks activated the PFN in a somatotopic fashion, whereby the semantic generation to leg stimuli activated regions proximal to where leg is located along the motor cortex (Figures 9b and 10b). Furthermore, shared activation was found for the leg motor localization and semantic generation tasks in the PFN and was organized somatotopically (Figures 9a and 10a). Finally, these results show both shared and unique activation in the PFN for pictures and words (Figure 11).

Figure 9: Leg (a) Shared and (b) Unique Activation for the Motor Localization and Picture Semantic Generation Tasks (area included in the ellipses)

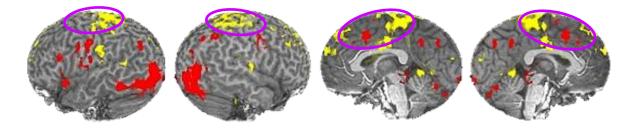
(a) Shared activation



Activation shared between the motor localization and semantic generation to leg picture stimuli (green coded activation) was found in the left SFG, precentral gyrus, SPL, MFG, SG, and AG on the lateral surface, and the left SMA, precentral gyrus, postcentral gyrus, cingulate gyrus (CG) and precuneus along the midline. In the right hemisphere, shared activation between the motor localization and semantic generation to leg picture stimuli was found in the SFG, precentral gyrus, and SPL on the lateral surface, and the SMA, precentral gyrus, postcentral gyrus, and precuneus along the midline.

Regions of activation shared between the motor localization and the semantic generation to leg picture stimuli outside the parietal-frontocentral network were found in the bilateral ITG, MTG, STG, and LOG on the lateral surface, and the bilateral cuneus, cerebellum and thalamus along the midline.

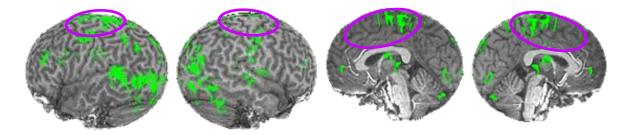
(b) Unique activation



Activation unique to the motor localization task (yellow coded activation) was found in the left precentral and postcentral gyri on the lateral surface, and the left precentral gyrus, postcentral gyrus, SMA, SFG, CG, and cuneus along the midline. In the right hemisphere, activation unique to the motor localization task was found in the precentral and postcentral gyri on the lateral surface, and the precentral gyrus, postcentral gyrus, SMA, SFG, and CG along the midline. For the semantic generation to leg picture stimuli (red coded activation), activation was found in the left premotor cortex, precentral gyrus, MFG, IFG pars triangularis, and AG on the lateral surface, and the left SMA, SFG, and precuneus along the midline. In the right hemisphere, activation unique to the semantic generation to leg picture stimuli was found in the premotor cortex and SPL in the lateral surface, and the SMA, SFG, and precuneus along the midline.

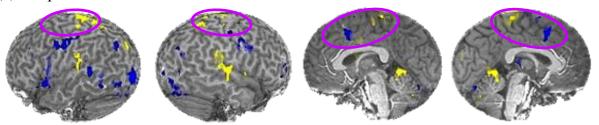
Regions of unique activation for the semantic generation to leg picture stimuli outside the parietalfrontocentral network were found in the ITG and MTG on the lateral surface of the left hemisphere and the LOG on the lateral surface in the right hemisphere, and the bilateral cuneus and cerebellum along the midline. Figure 10: Leg (a) Shared and (b) Unique Activation for the Motor Localization and Word Semantic Generation Tasks (area included in the ellipses)

(a) Shared activation



Shared activation between the motor localization and semantic generation to leg word stimuli (green coded activation) was found in the MFG, precentral gyrus, postcentral gyrus, SPL, AG, and SG on the lateral surface, and the SFG, SMA, precentral gyrus, postcentral gyrus, precuneus, and CG along the midline. In the right hemisphere, shared activation for the motor localilzation and semantic generation to leg word stimuli was found in the MFG, precentral gyrus, postcentral gyrus, postcentral gyrus, and FG pars opercularis on the lateral surface, and the SFG, SMA, precentral gyrus, and postcentral gyrus along the midline.

Regions of shared activation between the motor localization and semantic generation to leg word stimuli outside the parietal-frontocentral network were found in the bilateral STG, ITG, and LOG, the left MTG, and the right cerebellum on the lateral surface. Regions of shared activation between the motor localization and semantic generation to leg word stimuli outside the parietal-frontocentral network along the midline were found in the bilateral cuneus, cerebellum, and thalamus.

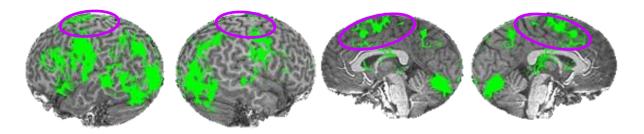


Activation unique to the motor localization task (yellow coded activation) was found in the left precentral gyrus and postcentral gyrus on the lateral surface, and the left SMA, precentral gyrus, and postcentral gyrus along the midline. In the right hemisphere, activation unique to the motor localization task was found in the precentral and postcentral gyri on the lateral surface, and the precentral and postcentral gyri along the midline. For the semantic generation to leg word stimuli (blue coded activation), activation was found in the left premotor cortex, MFG, precentral gyrus, IFG pars opercularis, and AG on the lateral surface, and the left CG, SFG, and SMA along the midline. In the right hemisphere, unique activation for the semantic generation to leg word stimuli was found in the premotor cortex, MFG, and precentral gyrus on the lateral surface, and the CG and SFG along the midline.

Regions of unique activation for the semantic generation to leg word stimuli outside the parietalfrontocentral network were found in the bilateral LOG, and the left STG, MTG, and ITG on the lateral surface.

(b) Unique activation

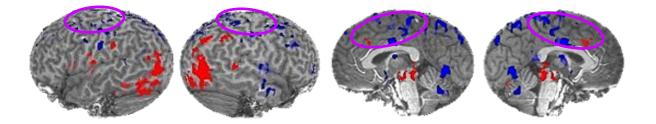
Figure 11: Leg (a) Shared and (b) Unique Activation for the Picture and Word Semantic Generation Tasks (area included in the ellipses) (a) Shared activation



Shared activation between the semantic generation to leg picture stimuli and leg word stimuli (green coded activation) was found in the left MFG, IFG, SFG, precentral gyrus, postcentral gyrus, and SPL on the lateral surface, and the SFG, SMA, CG, precentral gyrus, postcentral gyrus, and precuneus along the midline. In the right hemisphere, shared activation for the semantic generation to leg picture stimuli and leg word stimuli was found in the IFG pars triangularis, precentral gyrus, postcentral gyrus, and SPL on the lateral surface, and the right SFG, SMA, cingulate gyrus, precentral gyrus, precuneus, and cuneus along the midline.

Regions of shared activation for the semantic generation to leg picture and word stimuli outside the parietal-frontocentral network were found in the bilateral STG, ITG, and LOG, and the left MTG on the lateral surface, and the bilateral cerebellum, cuneus and thalamus along the midline.

(b) Unique activation



For the semantic generation to leg picture stimuli (red coded activation), activation was found in the left IFG and SG on the lateral surface, and the SFG and CG along the midline. In the right hemisphere, unique activation for the semantic generation to leg picture stimuli was found in the SPL on the lateral surface, and the SFG and CG along the midline. For the semantic generation to leg word stimuli (blue coded activation), unique activation was found in the MFG, precentral gyrus, postcentral gyrus, and SPL on the lateral surface, and the left SFG, SMA, CG, and precuneus, along the midline. In the right hemisphere, unique activation for the semantic generation to leg word stimuli was found in the MFG, postcentral gyrus, and SPL on the lateral surface, and the SFG, SMA, CG, and precuneus along the midline.

Regions of unique activation for the semantic generation to leg picture stimuli outside the parietalfrontocentral network were found in the bilateral LOG, the left ITG and MTG, and the right STG on the lateral surface and the bilateral cuneus and midbrain along the midline. Regions of unique activation for the semantic generation to leg word stimuli outside the parietal-frontocentral network were found in the right anterior temporal lobe and MTG on the lateral surface, and the bilateral cuneus and cerebellum along the midline.

Chapter 3 General Discussion

Comparison of the Motor and Semantic Generation Tasks

The results from the experiments in Chapter 3 show that the motor localization tasks activated regions along the motor cortex in accordance with Penfield's map of the motor homunculus (Penfield & Boldrey, 1937). Specifically, in the motor localization task, the fingertouch task produced unique activation in the dorsolateral motor cortex (Figure 6b and 7b), while the foot-pedaling task produced unique activation in the motor cortex along the midline (Figure 9b and 10b). In the semantic generation tasks, when participants described how they would interact with arm stimuli presented in both picture and word format there was a dorsolateral network of activation that included the posterior parietal cortex through to the premotor cortex and middle frontal gyrus (Figure 6b and 7b). When participants responded to how they would interact with leg stimuli presented in both picture and word format there was a medial dorsal network of activation from the posterior parietal cortex through to the supplementary motor area, premotor cortex and superior frontal gyrus (Figure 9b and 10b). As such, these results not only replicate earlier findings from the semantic generation task with words in Experiment 1, but also show that generating responses to picture stimuli activates regions proximal to the sensorimotor cortices. Additionally, a shared network of activation was shown between the arm motor localization and word semantic generation tasks in the PFN (Figure 6a and Figure 7a). The shared activation for arm word stimuli again replicated the results from Experiment 1.

In addition, the results showed a shared network of activation between the leg motor localization task and both the picture and word semantic generation tasks in the PFN (Figure 9a and 10a). The shared activation between the leg motor localization and word semantic generation tasks illustrates that when the sample size was increased, there were common regions of activation between these two tasks in the PFN. This suggests that the lack of shared activation between the leg motor localization and word semantic generation tasks in Experiment 1 was not necessarily due to having decreased complexity of action-related motor programs associated with legs, but may also have been due to a lack of power to pick up such an effect. The shared activation between the motor localization and semantic generation tasks was somatotopically organized, whereby arm stimuli activated the dorsalateral regions of the PFN, while leg stimuli activated the medial dorsal regions of the PFN. The shared activation between the motor localization and semantic generation tasks shows that the motor regions are activated during an

overt semantic generation task, and thus these results can be taken as further evidence in support of the theory of embodied cognition. The somatotopically organized shared activation in the PFN are also consistent with the hypothesis that regions that encode sensorimotor experiences are activated when retrieving action-related sensorimotor information, and moreover, it was shown that this activation occurs regardless of presentation format.

Although activation in the ventral processing stream (occipital-temporal cortices) was not the focus of these experiments, significant unique and shared activation for the semantic generation of pictures and words was found in the ventral stream, as is shown in Figures 6, 7, 9, and 10. Additionally, in the comparison of shared and unique activation for the semantic generation of pictures versus words, significant shared and unique activation was also found in the ventral stream (Figures 8 and 11). This is to be expected given previous research showing that the ventral stream processes semantic information (Martin, 2001; 2007; Martin & Chao, 2001). For example, previous research has shown that generating action words to visually presented pictures and words activates the middle temporal gyrus (Martin & Chao, 2001), while the loss of object knowledge has been associated with damage to the left posterior temporal cortex (Hart & Gordon, 1990). Furthermore, the investigation of somatotopic-semantics has found activation in the temporal regions when responding to literal (Raposo et al., 2009) and idiomatic action sentences (Boulenger et al., 2009) and when listening to action-related sentences (Tettamanti et al., 2005). Although, the ventral stream has been shown to be activated during object identification and during a number of different semantic tasks (Martin, 2007), and furthermore, that damage to the left temporal lobes has been associated with retrieving the names of objects, effector-specific somatotopic activation has not been shown in the ventral stream. This suggests that there is little involvement of the ventral stream in processing effector-specific semantic knowledge. Being that the goal of the current research is to provide an examination of embodied cognition by examining how the PFN is activated when participants provide their own knowledge of how to interact with an object (that is, whether there is evidence of somatotopicsemantic activation during an overt semantic generation task), and moreover, whether there are shared regions of activation between a semantic generation task and a motor localization task, the remainder of this discussion will focus on understanding activation in the parietal, sensorimotor and premotor cortices.

Neuroanatomical Support for Embodied Representations

As discussed in the introduction, embodied cognition theorists are interested in determining how the interaction between the body and environment shapes the human brain. According to Grafton (2009), embodied cognition is composed of a memory system that stores an individual's physical abilities and his or her capacity to interact within a physical environment. Furthermore, Gallese and Lakoff (2005) suggest that "conceptual knowledge is embodied", whereby conceptual knowledge is "mapped within our sensorimotor system" (pg. 456). Finally, Gallese and Lakoff purport that conceptual processing is bodily based, in that it makes use of our sensorimotor system via the simulation of action and perception (see also Svensson & Ziemke, 2004). For example, to understand a concept such as grasp, one must be able to simulate the action that goes along with *grasping* and the perceptual experience of grasping (Gallese & Lakoff, 2005). As such, the neural structures that are responsible for processing action and perceptual information would also be responsible for the conceptual processing of action-related stimuli (Grafton, 2009; Svensson & Ziemke, 2004). Hence one would expect that if conceptual representations are grounded in sensorimotor processing, then there should be evidence of semantic representations activating regions that process sensorimotor information (Barsalou, 1999; 2008b). Thus one goal of the research reported in this chapter was to determine if the same brain regions that are activated during a body movement are activated when overtly producing a response of how to use an object referring to a body part, and additionally, to determine whether these regions respond regardless of the presentation format of the stimulus.

Previous neuroimaging research has shown a somatotopic semantic organization in the frontocentral network, during the processing of action-related stimuli (Boulenger et al., 2009; Hauk et al., 2004; Raposo et al., 2008; Tettamanti et al., 2005). Furthermore, Hauk et al. (2004) have shown common regions of activation in the motor cortex between a motor localization task and a silent action word reading task that is somatotopically organized. The experiments in this chapter sought to further examine the theory of embodied cognition to determine whether there were common, or shared, regions of activation between the motor and semantic generation tasks regardless of presentation format. Given that embodied cognition theories state that the retrieval of action-related semantic information requires the simulation of sensorimotor experiences, then evidence of both shared regions (that is, common brain regions activated for both the motor and

semantic generation tasks) and unique regions (that is, unique activation for the motor localization or semantic generation tasks) of activation proximal to the sensorimotor cortices relevant to the effector involved, could be taken as evidence consistent with embodied cognition. The results demonstrated that there was shared activation in the PFN for the semantic generation and motor localization tasks. Additionally, the comparisons between the arm and leg motor localization and semantic generation tasks showed that generating responses to arm and leg stimuli activated regions proximal to the sensorimotor and premotor cortices in a somatotopic fashion. As such, these results provide neuroanatomical evidence that is consistent with the theory of embodied cognition, but additionally show that embodied processing occurs in these regions regardless of the presentation format of the stimulus. That is, the PFN responds to actionrelated stimuli independent of how this knowledge or information is stimulated. *Evidence of a Human Mirror Neuron System*

The results from this chapter may also be interpreted as consistent with the suggestion of a human mirror neuron system that responds during action-related language processing. Mirror neurons were originally found by a group of Italian researchers who were examining hand action movements in primates (di Pallegrino et al., 1992; Gallese et al., 1996; Rizzolatti et al., 1996). The researchers had placed electrodes in the primate premotor cortex, specifically area F5. Area F5 was shown to be activated during hand and mouth movements in primates; and furthermore, was shown to be somatotopically organized, whereby hand movements activate dorsal portions of area F5, while mouth movements activate ventral portions of area F5 (Rizzolatti et al., 1996). The researchers found that when the monkey carried out a goal-directed hand movement, neurons in area F5 fired (Rizzolatti et al., 1996). Interestingly, when the monkey observed the experimenter carrying out the same goal-directed hand movement, a portion of these same neurons also fired (Rizzolatti et al., 1996). Research has now shown that area F5 in primates is similar to Broca's area in humans (Fogassi & Ferrari, 2007; Rizzolatti and Craghero, 2004). As such, research is now being done to determine whether regions in the human premotor and motor cortices show the same mirror properties as those found in primates. Previous neuroimaging research has also shown evidence of a MNS in humans (Aziz-Zadeh et al., 2006b; Fadiga, Fogassi, Pavesi, and Rizzolatti, 1995; Rizzolatti and Craighero, 2004). For example, Aziz-Zadeh et al. (2006b) showed bilateral activation of the human MNS when participants observed, imitated, and executed a hand action. Some research suggests that the MNS may have evolved

from communicative gestures to facilitate language in humans (Rizzolatti & Craighero, 2004). Evidence of this has come from studies showing premotor cortex activation when participants process action-related language (Boulenger et al., 2009; Hauk et al., 2004; Tettamanti et al., 2005). The current results demonstrating significant shared activation between the motor localization and semantic generation tasks further support this notion, and additionally suggest that the same regions involved in the MNS may also be part of the PFN activated when people respond to action-related language. That is, these results illustrate that the motor regions that are activated when participants engage in overt hand and foot movements are also activated when participants provide responses to how they would interact with arm/hand and leg/foot stimuli. This indicates that the regions involved in the MNS may not only be activated when observing, executing, or imitating an action (Aziz-Zadeh et al., 2006b), but also overlap with the PFN when participants generate responses to how they would interact with objects used by specific body parts. Being that our understanding of conceptual information lies in our ability to simulate an action or interaction with a given concept (Gallese & Lakoff, 2005), and that the human MNS is putatively what makes action simulation possible (Grafton, 2009), then it is possible that this system could also be involved when responding to language referring to simulating actions. However, given that the identification of mirror neurons requires the same regions to be activated during action observation and action execution, future research should examine whether regions within the MNS that are activated during the semantic generation and motor localization tasks, are also activated when observing the same actions. This comparison would enable researchers to determine whether the MNS is in fact activated during action-related language processing.

Processing of Picture and Word Stimuli in the PFN

Previous patient research has suggested that pictures and words have differential access to semantic knowledge. Specifically, patient research has shown a dissociation between picture and word comprehension, whereby some patients show deficits in comprehending information presented in picture format, while others show deficits in comprehending information presented in word format (Bub et al., 1988; Lambon Ralph & Howard, 2000; Lhermitte & Beauvois, 1973). Furthermore, neuroimaging research has shown that pictures and words are processed in both modular (unique) and common (shared) brain regions (Borowsky et al., 2005a; Vandenberghe et al., 1996). Based on these studies, it was predicted that since pictures and words both have access

to action-related semantic information, and have been shown to be processed in common brain regions, then pictures and words should show shared regions of activation in the PFN. However, given that patients have shown a dissociation between the processing of pictures and words, and that pictures and words have been shown to be processed in unique brain regions, then there should also be unique activation found in the PFN. As such, another goal of the research reported in this chapter was to examine: (1) whether pictures and words were processed in the same regions, as shown by shared activation; (2) whether they are processed in separate regions, as shown by unique activation; or (3) whether pictures and words were processed in both shared and unique regions, which would support the notion that modular versus shared activation is not either-or, but may be best thought of as a gradient or continuum. As shown in Figure 8a and 11a, there is substantial shared activation in the PFN between pictures and words, demonstrating that both stimuli formats have access to shared action-related semantic representations in the PFN. However, these results also show unique activation between pictures and words in the PFN, suggesting that pictures and words are also processed in modular systems proximal to the motor cortex (Figures 8b and 11b). The unique activation within the PFN for pictures and words may be suggestive of pictures and words being processed in modular semantic systems. However, future research should compare the processing of a semantic task (e.g., semantic generation task) to a similar task with little semantic involvement (e.g., naming task) to determine whether unique activation in these regions is a function of the presentation format of the stimulus, or a function of semantic processing. Taken together, these results show that there is shared and unique activation for pictures and words, thus suggesting that action-related picture and word stimuli are processed in a shared semantic system, but also suggest that some parts of the PFN are activated specifically dependent upon stimulus format.

Conclusion

The results from Chapter 3 show that the semantic generation tasks activate the PFN in a somatotopic fashion regardless of presentation format. Moreover, shared activation was found in the PFN between the arm and leg motor localization and picture and word semantic generation tasks that was somatotopically organized, whereby shared activation was found proximal to where arms and legs are represented along the sensorimotor cortices. This suggests that the sensorimotor regions that encode action-related information are simulated when retrieving action-related semantic information. Taken together, these results provide neuroanatomical

evidence that is consistent with the theory of embodied cognition; and furthermore, that the PFN processes action-related semantic information regardless of whether the stimulus is presented in picture or word format.

CHAPTER 4

A BEHAVIOURAL EXAMINATION OF THE PROCESSING OF ACTION-RELATED STIMULI IN A GROUP OF CONTROL PARTICIPANTS AND POST-RIGHT AND POST-LEFT HEMISPHERECOMY

Portions of this chapter have been accepted for publication:

Esopenko, C., Crossley, M., Haugrud, N., & Borowsky. (in press). Naming and Semantic Processing of Action-Related Stimuli Following Right versus Left Hemispherectomy. *Submitted to Epilepsy and Behavior*, doi: 10.1016/j.yebeh.2011.06.017

The goal of Chapter 4 is to provide a behavioural examination of the processing of action-related stimuli. This chapter will: (1) examine the behavioural processing (response times and accuracy) of action-related picture and word stimuli in a group of normal healthy (control) participants; (2) compare the processing of action-related picture and word stimuli in tasks that differ in semantic complexity (that is, a naming versus semantic generation task); (3) examine the behavioural processing of action-related picture and word stimuli in an individual post-left hemispherectomy and in an individual post-right hemispherectomy; (4) compare the processing of action-related picture and word stimuli in semantic complexity post left versus post right hemispherectomy; and (5) examine whether there are differences in the processing of action-related picture and word stimuli in a naming and semantic generation task between the control group and post hemispherectomy.

Previous behavioural research has also provided evidence in favour of the theory of embodied cognition. Specifically, research has shown that the motor information represented in a sentence/word can influence responding (Glenburg & Kaschak, 2002), and that the degree of embodiment of a stimulus (as measured by body-object interaction (BOI) ratings) affects processing, with individuals being able to respond faster and more accurately to stimuli that are rated as more embodied (Siakaluk et al. 2008a; 2008b). Moreover, behavioural research has shown that stimuli presented in different presentation formats have differential access to actionrelated semantic information (Chainey & Humphreys, 2002; Saffran et al., 2003; Thompson-Schill et al., 2006). Specifically behavioural research has demonstrated that during verb generation tasks, a greater proportion of verbs are generated for pictures compared to words, thus suggesting that pictures have privileged access to action-related semantic knowledge, whereas

words have privileged access to word-associated knowledge (e.g., orthography and phonology). Taken together, these results provide behavioural evidence that semantic processing is grounded in sensorimotor experiences. Furthermore, these results suggest that pictures and words have access to different attributes or semantic representations, with differences in accessibility to action-related semantic knowledge dependent upon whether this information is accessed via pictures versus words.

Processing of Semantic Knowledge in Patients

Patient research has allowed us to examine how damage to a specific brain region can cause deficits in the processing or retrieval of semantic knowledge. For example, patient studies have illustrated that damage to the left prefrontal cortex produced word retrieval difficulties, suggesting that this region has a role in semantic processing (Martin & Chao, 2001). Damage to the left temporal lobes, on the other hand, are associated with difficulties in retrieving the names of objects, suggesting that object-specific semantic information is stored in the temporal lobes (Martin & Chao, 2001). Previous neuroimaging research on healthy participants has also provided evidence of left hemisphere dominance during the processing of semantic information (Chao & Martin, 2000; Martin, 2007; Martin et al., 1995; 1996). The functional neuroimaging results coincide with patient studies that illustrate that these regions are critical for storing representations about objects given that focal damage to these regions is associated with a loss of conceptual object knowledge (Hart & Gordon, 1990).

In addition, previous research examining the processing of action-related stimuli has shown deficits in patients when responding to action-related stimuli, and that such deficits coincide with damage to the premotor and frontotemporal cortices (with left > right atrophy), left prefrontal regions, and connections between the frontal regions and midbrain structures responsible for motor processing (Bak et al., 2001; Boulenger et al., 2008; Cotelli et al., 2006a; 2006b). These findings suggest that damage to regions that process motor information is associated with impairments in responding to motor-related, or action-related, language. As such, damage to the left hemisphere has been associated with deficits in the processing of semantic information; and moreover, that damage to the motor system (left more so than right) has been associated with deficits in the processing of action-related semantic information.

Examining the Sufficiency versus Necessity of Specific Brain Regions to Cognitive Function

One goal of Chapter 4 is to examine the necessity versus sufficiency of functioning during the processing of action-related stimuli. Although, previous neuroimaging research on healthy normal participants has shown left hemisphere dominance during the processing of action-related semantic information, Price et al. (2006) have cogently argued that such neuroimaging research on normal individuals can show us what regions may be *sufficient* for a specific task or function. However, according to Price and colleagues, the only way to determine whether a brain region is *necessary* to perform a given task or function is through a lesion to the brain region that is associated with a deficit in performing the task. Thus, necessity can only be established when damage occurs to a system or region and results in an impairment in performance that falls well outside normal levels of performance. Given that previous research has shown left hemisphere dominance during the processing of action-related semantic information (Esopenko et al., 2008; Hauk et al., 2004; Tettamanti et al., 2005), and that patients with damage to the motor, premotor, and motor pathways show deficits in responding to actionrelated language (e.g., Bak et al., 2001; Boulenger et al., 2008; Cotelli et al., 2006a; 2006b), it would be interesting to examine the processing of action-related stimuli post-left and post-right hemispherectomy to further explore the question of necessity versus sufficiency of function of the left versus right hemisphere brain regions for semantic processing. As such, in Experiments 4-6 the processing of action-related stimuli was examined in an individual post-left and an individual post-right hemispherectomy, and their performance was compared to normal controls, as a means to evaluate the necessity of the left versus right hemispheres in the processing of action-related semantic stimuli.

Summary and Hypotheses

Previous patient research suggests that pictures and words have differential access to semantic information, with pictures having privileged access to action-related semantic information and words having privileged access to word-associated information. Thus, control participants should perform better on the picture version of the semantic generation task, and should perform better on the word version of the naming task. As such, Experiments 4-6 will examine whether there are differences between performance on picture and word stimuli in the semantic generation and naming tasks; and furthermore, will examine whether there are differences in performance dependent upon whether participants are responding to arm/hand or

leg/foot stimuli. Finally, a comparison will be done between presentation format (pictures versus words) and stimulus type (arm versus leg) to determine whether there are differences in performance dependent upon presentation format and stimuli type.

In addition, Experiments 4-6, will examine the processing of action-related stimuli in an individual post-right and post-left hemispherectomy. The hemispherectomy participants completed the same tasks as the control participants to determine whether performance during the processing of action-related stimuli was affected by the removal of an entire hemisphere. This enabled the examination of the necessity versus sufficiency of the left and right hemispheres during the processing of action-related stimuli. Research has shown that: 1) the processing of semantic information shows left dominant processing (Martin, 2007; Martin & Caramazza, 2003; Martin & Chao, 2001); 2) action-related word stimuli elicit left dominant processing in the PFN that is somatotopically organized (as shown in Chapter 2; Hauk et al., 2004); 3) arm stimuli are processed bilaterally in the PFN (as shown in Chapter 2 and 3; Hauk et al.); and 4) processing of leg stimuli are mainly lateralized to the left hemisphere in the PFN (as shown in Chapter 2 and 3; Hauk et al.). As such, it was hypothesized that: (1) the individual post-right hemispherectomy (intact left hemisphere) would perform better overall; and (2) if the processing of leg stimuli is more lateralized to the left hemisphere, then the individual with the intact left hemisphere should perform better during the processing of leg stimuli, specifically.

Experiment 4

In Experiment 4, participants completed a behavioural variant of the arm picture and word semantic generation task discussed in Chapters 2 and 3. The first goal of Experiment 4 was to provide a behavioural examination of the processing of pictures and words in the semantic generation task using arm/hand stimuli. The second goal of Experiment 4 was to provide a behavioural examination of the processing of pictures and words in a semantic generation task using arm/hand stimuli in an individual post-left hemispherectomy and an individual post-right hemispherectomy.

Materials and Methods

Participants

S.M. (right hemispherectomy, intact left hemisphere; 52 years of age) began experiencing seizures at age 5 and a left-sided hemiparesis at age 6. At age 6 she had a right frontoparietal craniotomy to remove a lesion in the right primary motor area (M1) to treat her drug-resistant seizures. By age 13 S.M. was having daily generalized tonic-clonic seizures (also referred to as grand mal seizures and affect the entire brain) and therefore underwent a complete anatomic right-sided hemispherectomy. Post hemispherectomy, S.M.'s seizure frequency (and severity) was greatly reduced, but she still continued to experience complex partial seizures (seizures localized to a particular lobe and associated with a loss of consciousness) approximately 1-2 times per week and receives anticonvulsant therapy (Fournier, Calverley, Wagner, Poock, & Crossley, 2008; Cummine, Borowsky, Stockdale Winder & Crossley, 2009).

J.H. (left hemispherectomy, intact right hemisphere; 54 years of age) was noted to have a right-sided hemiparesis shortly after birth, and began experiencing simple partial motor seizures (seizures localized to the temporal lobe where she would experience an aura but no loss of consciousness) at the age of 8 that progressed into generalized tonic-clonic seizures and by 16 years of age she was experiencing 30 generalized tonic-clonic seizures per day. At age 16 she had a full anatomic left-sided hemispherectomy to treat her drug-resistant seizures. The hemispherectomy resulted in complete abatement of seizures and her anticonvulsant treatment was terminated within one year post-surgery (Fournier et al., 2008; Cummine et al., 2009). Both hemispherectomy participants have corrected to normal vision.

The control participants (N = 56; mean age = 19.6) were healthy undergraduate students participating for course credit in their introductory psychology class. They had English as a first

language and normal or corrected to normal vision. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences Ethics Committee.

Stimuli and Procedure

All participants completed a picture and word arm/hand semantic generation task. The stimuli consisted of 25 pictures and words referring to objects that are typically used by the arm/hand (see Appendix A). Pictures or words were presented on the screen and participants were instructed to describe quickly and accurately how they would interact with the presented object (e.g., pen: "write" or "write with it"). For the control participants the picture and word tasks were counterbalanced across participants. J.H. and S.M. completed the same tasks as the controls, with the exception that both participants saw the picture version of the task first. Because there were only two hemipsherectomy participants, the presentation format of the stimuli was kept consistent to allow for direct comparisons between patients. Stimuli were presented on the screen (IBM E94 monitor) until participants finished responding. Onset times (indicated by voice key onset) were measured via a microphone interfaced with the computer through the EPrime serial response box. The onset response time consisted of the time from when the stimulus appeared on the screen until the onset of an individual's verbal response. Vocalization response times (when the participant finished speaking) were recorded via a button press by the experimenter. The total duration to respond (TDR) was determined by summing the onset response time and vocalization response time (Esopenko et al., 2008). Responses were coded as accurate if participants provided a correct use for the object.

Results

Control Participants Analysis

For calculating mean TDR only correct responses were used, and if control participants' mean trial TDRs or accuracy were greater than \pm 3 standard deviations (SD) from the mean of the control participants, they were not included in the TDR and accuracy analyses. This resulted in four participants' data not being included in the arm semantic generation task analysis. Mean TDR and accuracy for the arm semantic generation task are also shown in Table 1. A paired comparison between the dependent variables of TDR and accuracy in the arm pictures and arm words conditions was carried out. The analysis showed that participants responded marginally faster to pictures (M = 1568.11 msec) compared to words (M = 1651.34 msec) in the semantic

generation task, t(51) = 1.765, p = .084. There were no differences in accuracy rates between pictures (M = .953) and words (M = .953) in the semantic generation task, t(51) = .101, p = .920. As such, these results demonstrate that pictures access action-related semantic information faster than words, but that the effect was only marginally significant (but would be significant by a one-tailed test, which can be argued as appropriate here given that the effect was predicted to favour pictures)¹.

Table 1. (A) Mean Total Duration to Respond (TDR, in milliseconds) and (B) Accuracy for the Arm Semantic Generation to Pictures and Words.

A)		

Stimuli Type	Words (std.dev)	Pictures (std.dev)
Arm Stimuli		
a) Controls	1651 (317)	1568 (282)
b) J.H.	3252	2511
c) S.M.	2709	3243
B)		
B)		
Stimuli Type	Words (std.dev)	Pictures (std.dev)
,	· · · · · · · · · · · · · · · · · · ·	· · · · · · · · · · · · · · · · · · ·
Stimuli Type	Words (std.dev) .95 (.050)	Pictures (std.dev) .95 (.049)
Stimuli Type Arm Stimuli	· · · · · · · · · · · · · · · · · · ·	· · · · · · · · · · · · · · · · · · ·

To further examine differences between the means in the arm semantic generation task, confidence intervals were computed based on the method described by Loftus and Masson (1994). The Loftus and Masson confidence intervals have more power to detect differences than a paired t-test because it is based on the within-subject error. Thus the Loftus and Masson confidence intervals were used to provide a more rigorous examination of the mean differences between tasks. These confidence intervals allow one to determine whether the mean of one

¹One stimulus in the arm semantic generation task was found to have an unusual spelling, although still phonologically correct (i.e., Badminton Racquet was spelled Badminton Raquet); however none of the participants reported noticing the spelling. Nonetheless, this same analysis was run with this stimulus removed to determine whether the inclusion of this stimulus would have affected the outcome of the analysis. The pattern of results remained the same, whereby participants responded marginally faster to pictures compared to words, t (51) = 1.953, p = .056, and there were no differences between presentation format on accuracy rates, t (51) = .105, p = .917.

condition falls outside the confidence intervals as computed using the mean square error (MSe) from a simple repeated measures analysis of variance (ANOVA). If one mean falls outside the confidence interval of another, then the means are significantly different from one-another. As such, a simple repeated measures ANOVA was computed to provide the appropriate MSe for the calculation of the Loftus and Masson 95% confidence intervals. The equation used for this analysis, corresponding confidence intervals and mean differences are shown in Table 2. A simple repeated measures ANOVA examining differences between the TDR for pictures and words showed a marginal difference in TDR, F(1,51) = 3.114, p = .084, which is the identical outcome as the earlier *t*-test, illustrating that both tests are based on the same general linear model test ($t^2 = F$). The confidence interval computed from the simple repeated measures ANOVA was \pm 47.3 msec, and the mean difference between the TDR for the picture and word tasks was 83 msec. This shows that the mean difference falls outside the confidence interval for the task, which indicates that the means were significantly different from one another. The same analysis was carried out for accuracy and showed no difference in participants' accuracy for pictures and words, F(1,51) = .010, p = .920. The confidence interval analysis shows that the mean difference falls within the confidence interval for the task indicating that the means between the tasks were not significantly different from each other.

Table 2. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format for the Arm Semantic Generation Tasks.

Stimuli Type	Dependent Variable	Words	Pictures	Confidence Interval	Mean Difference
Arm	a) TDR (msec)	1651	1568	47.3	83 *
	b) ACC	.95	.95	.009	0

Note. The confidence intervals were computed using the following formula from Loftus and Masson (1994):

 $CI = M_j \pm \sqrt{MSe/n [critical t (df MSe)]}$

If the mean of one condition is outside the 95% confidence interval of the other condition's mean, then the difference is considered to be statistically significant (Masson & Loftus, 1994), whereas if the mean difference between the tasks is within the confidence interval, then the comparison is not significant.

* = mean difference is significant.

Hemispherectomy Participants Analysis

Mean TDR and accuracy for the arm semantic generation task are also shown in Table 1. A comparison between the hemispherectomy participants and the control group is shown in Figure 12. For the hemispherectomy participants to be impaired on the task, their mean TDR and accuracy scores must fall beyond approximately 2 SD from the control group (i.e., z > 1.96, p < .05). For the arm semantic generation task, S.M. was faster at generating a response to words (M = 2709 msec) compared to pictures (M = 3243 msec), but was more accurate responding to pictures (M = .84) compared to words (M = .76). When compared to control participants' mean TDR, S.M. was 3.34 SD slower than controls when generating a response to words, and was 5.94 SD slower than controls when generating a response to pictures. When compared to control participants' mean accuracy when generating a response to words, and was 2.24 SD less accurate than control participants' accuracy when generating a response to pictures.

J.H. was faster at generating a response to pictures (M = 2511 msec) compared to words (M = 3252 msec), but was more accurate when responding to words (M = .92) compared to

pictures (M = .88). When compared to control participants' mean TDR, J.H. was 5.05 SD slower than controls when generating a response to words, and was 3.34 SD slower than controls when generating a response to pictures. When compared to control participants' mean accuracy scores, J.H. was .6 SD less accurate than control participants' accuracy when generating a response to words, and was 1.43 SD less accurate than control participants' accuracy when generating a response to pictures.

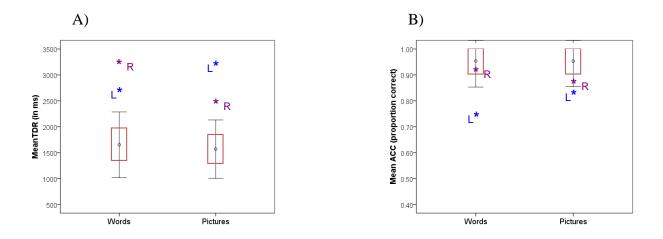


Figure 12. (A) Mean Total Duration to Respond (TDR, in milliseconds), and (B) Mean Accuracy (ACC, proportion correct) during the Arm Semantic Generation to Pictures and Words. L* has intact left hemisphere, *R has intact right hemisphere. Bar is ± 2 SD, box is ± 1 SD, around mean of normal controls.

Discussion

The results from the paired comparisons analysis show that control participants were marginally faster at responding to pictures compared to words, but showed no difference in accuracy rates between pictures and words. The analysis of confidence intervals demonstrates that control participants were significantly faster at responding to pictures, with no differences in accuracy. The results from the hemispherectomy participants show that S.M. was faster and less accurate at responding to arm word stimuli, while J.H. was slower and more accurate. Moreover, although both individuals are impaired on TDR when responding to arm picture stimuli, both individuals fall within, or close to, 2 SD of the controls' mean accuracy.

Experiment 5

In Experiment 5, participants completed a behavioural variant of the leg semantic generation task discussed in Chapters 2 and 3. The first goal of Experiment 5 was to provide a behavioural examination of the processing of pictures and words in the leg semantic generation task. The second goal of Experiment 5 was to provide a behavioural examination of the processing of pictures and words in the leg semantic generation task in an individual post-left hemispherectomy and an individual post-right hemispherectomy.

Materials and Methods

Participants

The same participants from Experiment 4 completed Experiment 5. *Stimuli and Procedure*

Participants completed a picture and word leg semantic generation task. The stimuli consisted of pictures and words referring to objects that are typically used by leg/feet (e.g., soccerball; see Appendix A). Pictures or words were presented on the screen and participants were instructed to describe quickly and accurately how they would interact with the presented object (e.g., soccerball: "kick it"). The same procedure from Experiment 4 was used in Experiment 5.

Results

Control Participants Analysis

For calculating mean TDR only correct responses were used, and if control participants' mean trial TDR or accuracy were greater than \pm 3 SD from the mean, they were not included in the TDR and accuracy analyses. This resulted in two control participants' data not being included in the leg semantic generation task analysis. Mean TDR and accuracy for the leg semantic generation task are also shown in Table 3. Due to improvements made to the stimuli set between the experiments in terms of changing unusual spellings or items that participants were not familiar with, five leg stimuli (Rollarskate, Rollarblade, Pogo Ball, Skip-it, and Kickball) were not included in the analysis. To be able to compare performance between the two experiments, only stimuli that were responded to in both experiments were included. The results from Experiment 5 show that there were no differences in how quickly participants responded to pictures (M = 1576.17 msec) compared to words (M = 1641.38 msec) in the semantic generation

task, t (53) = 1.552, p = .127. There were no differences in accuracy rates between pictures (M = .944) and words (M = .941) in the semantic generation task, t (53) = -.356, p = .723.²

Table 3. (A) Mean TDR (in milliseconds) and (B) Accuracy for the Leg Semantic Generation to Pictures and Words.

Stimuli Type	Words (std.dev)	Pictures (std.dev)
Leg Stimuli		
a) Controls	1641 (380)	1576 (301)
b) J.H.	2656	3437
c) S.M.	2223	2708

Stimuli Type	Words (std.dev)	Pictures (std.dev)
Leg Stimuli		
a) Controls	.94 (.069)	.94 (.052)
b) J.H.	.85	.70
c) S.M.	.80	.90

As in the arm semantic generation task, a simple repeated measures ANOVA was carried out to examine differences between the TDR for words and pictures in the leg semantic generation task. The confidence intervals and mean differences for the analyses can be found in Table 4. The simple repeated measures ANOVA examining differences in TDR for words and pictures was not significant, F(1,53) = 2.408, p = .127. The confidence interval computed from

² Three stimuli in the leg semantic generation task were found to have an unusual spelling, although still phonologically correct (i.e., Rollerblade was spelled "Rollarblade", Roller Skate was spelled "Rollarskate", and Sandal was spelled "Sandel"); however none of the participants reported noticing the spelling. Furthermore, three stimuli (Pogo Ball, Kickball, and Skip-it) were not included in the naming experiment due to other experiments from our laboratory showing that participants have difficulty responding to these stimuli due to a lack of familiarity with the stimuli. As such, this same paired-comparison analysis was run with these stimuli removed to determine whether this affected the results. The results from this analysis show that there were no significant differences in TDR between pictures and words in the leg semantic generation task, t (53) = 1.627, p = .110, and for accuracy, t (53) = -.444, p = .659. Thus, the results from the analysis with all 6 stimuli removed show the same effects as the analysis reported in the text.

The same analysis was also carried out with all stimuli included to examine whether there were differences between the 5 stimuli removed analysis as reported in the text and the inclusion of all stimuli. The results show no significant differences between pictures and words on TDR, t(53) = 1.501, p = .139, but a marginal difference between pictures (M = .91) and words (.93) on accuracy, t(53) = 1.720, p = .091. As such, these TDR results show the same effects as the analysis reported in the text, whereby there were no differences in how quickly participants responded to pictures and words. However, with all stimuli included, participants were now marginally more accurate responding to words compared to pictures, whereas in the analysis reported in the text there were no significant differences on accuracy rates for pictures and words.

the simple repeated measures ANOVA was \pm 42.1 msec, and the difference between the TDR for pictures and words was 65 msec. This shows that the means were significantly different from each other. The simple repeated measures ANOVA examining differences between the accuracy for words and pictures was not significant, F(1,53) = .127, p = .723. The confidence interval computed from the simple repeated measures ANOVA was \pm .01, and the difference between the accuracy for pictures and words was zero, and so indicates that the means were not significantly different from each other.

Table 4. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format for the Leg Semantic Generation Tasks

Stimuli Type	Dependent Variable	Words	Pictures	Confidence Interval	Mean Difference
Leg	a) TDR (msec)	1641	1576	42.1	65 *
	b) ACC	.94	.94	.01	0

* = mean difference is significant.

Analysis of Experiment 4 (Arm Semantic Generation Task) and Experiment 5 (Leg Semantic Generation Task) in Control Participants. Given that the same participants completed the arm and leg semantic generation Experiments, differences between stimulus type and presentation format were examined. A simple repeated measures ANOVA with stimuli type (arm versus leg) and presentation format (pictures versus words) was used to determine whether there were differences in TDR and accuracy dependent upon stimulus type and presentation format. Five participants were not included in the analysis because either their TDR or accuracy fell outside of \pm 3 SD from the mean TDR or accuracy in one of more of the conditions. The same Loftus and Masson (1994) confidence intervals described above were used in this analysis to examine differences between means.

The simple repeated measures ANOVA for TDR was significant, suggesting there is at least one significant difference in TDR between the four conditions, F(3, 150) = 2.966, p = .034. The mean TDR for each condition, corresponding confidence intervals and mean differences between conditions are shown in Table 5. The results show that for both arm and leg stimuli, there were significant differences between pictures and words, with pictures being responded to significantly faster than words. In addition, the results show that for pictures and words, there

were no differences between the TDR for arm and leg stimuli. These results suggests that across stimuli type, pictures were responded to faster than words, and there were no differences in TDR dependent upon stimuli type when the stimulus was presented in the same format.

	Stimuli Type	Word Mean	Picture Mean	Confidence Interval	Mean Difference: Presentation Type
TDR (msec)	a) Arm	1648	1554	40.3	94 *
	b) Leg	1615	1544	40.3	71^*
Mean Difference: Stimulus Type	Arm – Leg	33	10		
ACC	a) Arm	.96	.96	.015	0
	b) Leg	.94	.94	.015	0
Mean	Arm - Leg	.02*	$.02^{*}$		
Difference: Stimulus Type					

Table 5. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format and Stimulus Type for the Semantic Generation Tasks

* = mean difference is significant.

The simple repeated measures ANOVA for accuracy was not significant, F(3,150) = 1.013, p = .389. The mean differences and corresponding confidence intervals between conditions are shown in Table 5. The results show that for arm and leg stimuli there were no significant differences in accuracy between pictures and words. When arm and leg stimuli were presented in the same presentation format, there were differences in accuracy for arm and leg stimuli. These results suggest that regardless of presentation format, arm stimuli were responded to more accurately than leg stimuli. As such, these results show that participants were more accurate when responding to arm stimuli; and furthermore, that the presentation format of a stimulus affects how quickly a participant responds, but does not affect the accuracy of the response.

Given that the Loftus and Masson (1994) confidence intervals showed differences in responding dependent upon presentation format for TDR and stimulus type for accuracy, a 2X2

repeated measures factorial ANOVA was also run to determine whether there was a significant interaction between stimulus type (arm versus leg) and presentation format (pictures versus words) in the semantic generation tasks. Mean TDR and accuracy are shown in Table 5. The ANOVA for TDR demonstrated that the main effect of stimulus type was not significant, F (1,50) = 1.033, p .314, whereas the main effect of presentation format was marginally significant, F (1,50) = 3.787, p = .057. The interaction was also not significant, F (1,50) = .545, p = .464. For accuracy, the ANOVA demonstrated that both the main effect of stimulus type, F (1,50) = 2.413, p = .127, and presentation format, F (1,50) = .027, p = .870, were not significant. In addition, the interaction was not significant, F (1,50) = .073, p = .788.

Hemispherectomy Participants Analysis

For calculating mean TDR in the leg semantic generation task, only correct responses were used. Mean TDR and accuracy for the leg semantic generation task are also shown in Table 3. Like in the arm semantic generation analyses, the hemispherectomy participants showed an impairment on task performance if their mean TDR and accuracy scores fell beyond 2 SD from the control group. Comparisons between the hemispherectomy participants' mean TDR and accuracy and the control participants are shown in Figure 13. For the leg semantic generation task, S.M. was faster at generating a response to words (M = 2223 msec) compared to pictures (M = 2708 msec), but was more accurate responding to pictures (M = .90) compared to words (M = .80). When compared to the control participants' mean TDR, S.M. was 1.53 SD slower than controls when generating a response to words, and was 3.76 SD slower than controls when generating a response to pictures. When compared to control participants are an accuracy scores, S.M. was 2.03 SD less accurate than control participants' accuracy when generating a response to words, and was 3.77 SD less accurate than control participants' accuracy when generating a response to pictures.

J.H. was faster at generating a response to words (M = 2656 msec) compared to pictures (M = 3437 msec), and was more accurate when generating a response to words (M = .85) compared to pictures (M = .70). When compared to control participants' mean TDR, J.H. was 2.67 SD slower than controls when generating a response to words, and was 6.18 SD slower than controls when generating a response to pictures. When compared to control participants' mean accuracy scores, J.H. was 1.30 SD less accurate than control participants' accuracy when generating a response to words, and was 4.62 SD less accurate than control participants'

accuracy when generating a response to pictures. Together these results suggest that both individuals showed an impairment on TDR; however, only J.H. shows an impairment on accuracy in the leg picture semantic generation task.

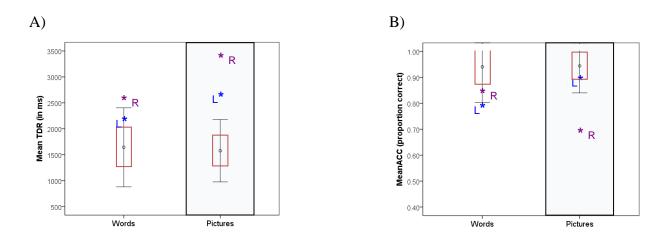


Figure 13. (A) Mean TDR (in milliseconds), and (B) Mean Accuracy (ACC, proportion correct) during the Leg Semantic Generation to Pictures and Words. L* has intact left hemisphere, *R has intact right hemisphere. Bar is ± 2 SD, box is ± 1 SD, around mean of normal controls.

Observation of Performance in the Hemispherectomy Participants

As shown above, S.M. and J.H. demonstrated differences in their ability to respond in the semantic generation tasks. Observation of both individuals completing the tasks also provided interesting insight into the differences in their functional abilities. For example, although S.M. was able to provide uses for both arm and leg picture and word stimuli, most responses were limited to single word responses. Furthermore, most of S.M.'s descriptions of object uses were from higher ordinate categories, such as: "play", "work", or "personal use". For picture stimuli, S.M. was able to provide more diverse uses compared to words, but was still limited to higher ordinate categories of object use. J.H. was also able to provide uses for arm picture and word stimuli, J.H. was able to give full sentence responses, which could account for her longer total duration to respond. However, for leg stimuli, she had difficulties completing the task. In the leg word condition, J.H. was limited to single word responses on most stimuli (e.g., "kick"). Thus, whereas for arm stimuli she was able to give full sentence responses of how to use an object, for leg word stimuli she was only able to provide

single word responses to most stimuli. This difficulty was even more pronounced for leg picture stimuli. Specifically, when J.H. was trying to produce a use for leg picture stimuli, it seemed as if she knew what the object was, but had difficulties being able to 'find' the use for a leg object. For some objects, J.H. would even try to act out how she would use them in order to find a way to verbally state the object's use. Thus, for leg picture stimuli, J.H. required a greater amount of search time to provide a use for an object, which could account for her longer total duration to respond to leg picture stimuli. As such, the subjective observation of both individuals is in line with the results from the analysis of response times. An analysis of median TDRs, which are unaffected by outlier TDRs, is reported in Experiment 6.

These results suggest that the differences in the TDR for the hemispherectomy participants may be due to two factors: 1) a longer TDR reflects a verbal response consisting of more than one word answers; or 2) a longer TDR reflects a struggle to produce a response for a stimulus. One way to determine which factor the longer TDR represents is to examine both response time and accuracy measures. Specifically, if the TDR is long, but the individual is accurate in their response, then this represents a multiple word response. However, if the TDR is long and the individual is not accurate in their response, then this suggests longer search times and a struggle to produce a response for the stimulus. This objective analysis is also consistent with the experimenter's subjective experience while testing these two participants. Thus, if an individual has a long mean TDR but is accurate in the task, then this is not an impairment, whereas if an individual has a long mean TDR and is inaccurate in the task, then this represents an impairment. As such, for arm stimuli, J.H. has a longer TDR, but is also quite accurate when responding, whereas for leg picture stimuli, J.H. has a longer TDR and is significantly less accurate when responding. Hence, for arm stimuli, taking into consideration both TDR and accuracy, J.H. is not impaired, however for leg picture stimuli, taking into consideration both TDR and accuracy, J.H. is impaired.

Discussion

The results from the paired comparisons showed no significant differences between pictures and words on TDR and accuracy. However, the analysis of confidence intervals showed that pictures were responded to faster than words. The analysis of arm and leg stimuli showed that participants were faster at responding to pictures compared to words regardless of stimulus type (arm versus leg). An examination of the results for the hemispherectomy participants

demonstrated that only leg picture stimuli elicited a consistent impairment across response time and accuracy. Specifically, the individual with an intact right hemisphere (J.H.) demonstrated an impairment on response time and accuracy, whereas the individual with an intact left hemisphere (S.M.) performed relatively close to normal limits on response time and accuracy. As such, a single dissociation was shown for the semantic generation to leg picture stimuli.

Experiment 6

The first goal of Experiment 6 was to provide a behavioural examination of the processing of pictures and words in a naming task. The second goal of Experiment 6 was to provide a behavioural examination of the processing of pictures and words in a naming task in an individual post-left hemispherectomy and an individual post-right hemispherectomy. Given that patient research typically assesses an individual's functioning based on the naming of objects and words, a naming task was included to measure the processing of the stimuli in a task that does not require a great deal of semantic processing to complete. As such, the results from the naming task, which requires less semantic knowledge to complete, will also be compared to the semantic generation task, which requires a greater amount of semantic knowledge to complete.

Materials and Methods

Participants

The same participants from Experiment 4 and 5 completed Experiment 6. *Stimuli and Procedure*

All participants completed a picture and word naming task. The order of the picture and word tasks was counterbalanced across participants. J.H. and S.M. completed the same tasks as the controls, and both participants completed the picture version of the task first to permit direct comparison of their results. The stimuli consisted of 50 pictures and words representing objects used by the arm/hand and leg/foot. Pictures or words were presented on the screen and participants were instructed to name the picture or word as quickly and accurately as possible. The procedure for both the controls and hemispherectomy participants were identical to Experiment 5, with the exception that arm/hand and leg/foot stimuli were presented together. Furthermore, three leg stimuli were changed because participants had difficulties responding to them in an earlier semantic generation experiment (Skip-it, Pogo Ball, and Kickball). Responses were coded as accurate if participants correctly named the picture or word stimulus.

Results

Control Participants Arm Stimuli Analysis

The same outlier procedure was used as in Experiment 4 and 5, resulting in two participants' data not being included in the arm naming task. Mean TDR and accuracy for the arm naming task are also shown in Table 6. The results from the naming of arm stimuli show that participants named words (M = 945.22 msec) significantly faster than pictures (M = 1172.38

msec), t(53) = -21.572, p < .001. There were no differences in accuracy rates between words (M = .981) and pictures (M = .984) in the arm naming task, t(53) = -.683, p = .498.³

Table 6. (A) Mean TDR (in milliseconds) and (B) Accuracy for the Naming of Pictures and Words.

A)

b) **J.H.**

c) S.M.

Stimuli Type	Words (std.dev.)	Pictures (std.dev)	
Arm Stimuli			
a) Controls	945 (104)	1172 (126)	
b) J.H.	1492	1974	
c) S.M.	1536	1916	
Leg Stimuli			
a) Controls	913 (113)	1252 (158)	
b) J.H.	1609	1905	
c) S.M.	1507	2279	
B)			
Stimuli Type	Words (std.dev)	Pictures (std.dev)	
Arm Stimuli			
a) Controls	.98 (.025)	.98 (.023)	
b) J.H.	.96	.88	
c) S.M.	.96	.80	
Leg Stimuli			
a) Controls	.97 (.030)	.94 (.059)	
- ·	· · · · ·	— a ` ´ ´	

A simple repeated measures ANOVA to compute the Loftus and Masson (1994) 95% confidence intervals as described above. The confidence intervals and mean differences for this analysis can be found in Table 7. The simple repeated measures ANOVA of TDR showed that words were responded to significantly faster than pictures, F(1,53) = 465.35, p < .001. The

.95

1

.70

.50

³ Like in Experiment 4, Badminton Racquet was found to have an unusual spelling in the naming task, although it was still phonologically correct ("Badminton Raquet"); however none of the participants reported noticing the spelling. The analysis with the stimulus removed showed the same pattern of significant and non-significant effects as those found in the analysis including this stimulus: TDR, t(53) = -22.530, p < .001, and accuracy, t(53) = -.683, p = .498. As such, this analysis shows that the inclusion this stimulus did not affect the outcome of the analysis.

confidence interval computed from the simple repeated measures ANOVA was \pm 10.56 msec, and the mean difference between the TDR for pictures and words was 227 msec. This shows that the mean difference is outside the confidence interval, which also indicates that the means were significantly different from each other. The simple repeated measures ANOVA examining accuracy for words and pictures was not significant, F(1,53) = .466, p = .498. The confidence interval computed from the simple repeated measures ANOVA was \pm .006, and the difference between the accuracy rates for pictures and words was zero, which indicates that the means were not significantly different from each other.

Table 7. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format for the Arm Naming Tasks

Stimuli Type	Dependent Variable	Words	Pictures	Confidence Interval	Mean Difference
Arm	a) TDR (msec)	945	1172	10.56	227^*
	b) ACC	.98	.98	.006	0

* = mean difference is significant.

Control Participants Leg Stimuli Analysis

The same outlier procedure was used as in Experiment 4 and 5, resulting in three participants' data were not being included in the leg naming task analysis. Mean TDR and accuracy for the leg naming task are also shown in Table 6. Due to changes in the stimuli set between Experiment 5 and Experiment 6, five stimuli (Roller Skate, Rollerblade, Bowling Shoes, Unicycle, and Scooter) were not included in the analyses, because they had been substituted for 5 stimuli that had been included in Experiment 5 (see Appendix A for a list of substituted stimuli). To be able to compare processing in the hemispherectomy participants between tasks, only the same stimuli that were responded to in both experiments are included. The results from the naming of leg stimuli show that participants named words (M = 912.88 msec) significantly faster than pictures (M = 1251.51 msec), t (52) = -25.441, p <.001, and were more accurate when naming words (M = .975) compared to pictures (M = .938), t (52) = 4.422, p <.001. Together,

these results show that words are named faster for both arm and leg stimuli; and moreover, that participants are also more accurate at naming leg word stimuli.⁴

Table 8. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format for the Leg Naming Tasks

Stimuli Type	Dependent Variable	Words	Pictures	Confidence Interval	Mean Difference
Leg	a) TDR (msec)	913	1252	13.34	339 *
_	b) ACC	.97	.94	.009	.03*

* = mean difference is significant.

A simple repeated measures ANOVA was carried out to examine differences between the TDR for words and pictures in the leg naming task. The confidence intervals and mean differences for this analysis can be found in Table 8. The simple repeated measures ANOVA of TDR showed that words were responded to significantly faster than pictures, F(1,52) = 647.23, p < .001. The confidence interval computed from the simple repeated measures ANOVA was \pm 13.34 msec, and the mean difference between the TDR for pictures and words was 339 msec. This shows that the mean difference is outside the confidence interval, which also indicates that the means were significantly different from each other. The simple repeated measures ANOVA examining accuracy showed that words were responded to more accurately than pictures, F(1,52) = 19.558, p < .001. The confidence interval computed from the simple repeated measures ANOVA examining accuracy showed that words were responded to more accurately than pictures, F(1,52) = 19.558, p < .001. The confidence interval computed from the simple repeated measures ANOVA was $\pm .009$, and the mean difference between the accuracy for pictures and words was .03. This shows that the mean difference is outside the confidence interval, which indicates that the means were significantly different from each other.

⁴ One stimulus in the leg naming task was found to have an unusual spelling, although still phonologically correct (i.e., Sandal was spelled "Sandel"); however none of the participants reported noticing the spelling. Furthermore, 5 other stimuli had been changed from the semantic generation task (Roller Skate, Rollerblade, Bowling Shoes, Scooter, and Unicycle) to replace the stimuli from the semantic generation task that participants had difficulty responding to due to a lack of familiarity with the stimuli. As such, this same paired comparison analysis as Experiment 6 was run with these 6 stimuli removed to determine whether inclusion of the stimuli affected the results of the experiment. The results from the 6 stimuli removed analysis shows significant differences between pictures and words on TDR and accuracy, thus showing the same effects as the analysis with 5 stimuli removed, respectively. The same analysis was also carried out with all stimuli included. The results show the same effects as those discussed with 5 and 6 stimuli removed.

Differences between Arm and Leg Stimuli in Experiment 6 (Naming Task) in Control Participants. Like the semantic generation tasks, the same participants completed the arm and leg naming tasks, and thus differences between stimulus type and presentation format could be examined. A simple repeated measures ANOVA with stimulus type (arm versus leg) and presentation format (pictures versus words) was used to determine whether there were differences in TDR and accuracy dependent upon stimulus type and presentation format. Again like in the semantic generation task, a simple repeated measures ANOVA was carried out to compute the Loftus and Masson (1994) confidence intervals to determine if the means were significantly different from one-another. In the naming analysis, five participants were not included in the analysis because either their TDR or accuracy fell outside of ± 3 SD from the mean TDR or accuracy in one of more of the conditions.

The simple repeated measures ANOVA for TDR was significant, suggesting there were differences in TDR between the four conditions, F(3, 150) = 445.34, p < .001. The results show that for both arm and leg stimuli, participants were significantly faster responding to words compared to pictures (see Table 9 for confidence intervals and mean differences between conditions). The results show an interaction between stimulus type and presentation format. Specifically, for words, participants were faster at responding to leg stimuli compared to arm stimuli, whereas for pictures, participants were faster at responding to arm stimuli compared to leg stimuli. These results suggest that regardless of stimulus type (arm versus leg), participants were faster when responding to words, and that there was an interaction found between stimulus type and presentation format (i.e., arm words > leg words; arm pictures < leg pictures).

	Stimuli	Word	Picture	Confidence	Mean Difference:
	Type	Mean	Mean	Interval	Presentation Type
TDR (msec)	a) Arm	943	1172	11.06	229 [*]
	b) Leg	907	1242	11.06	335 [*]
Mean Difference: Stimulus Type	Arm - Leg	36*	70*		
ACC	a) Arm	.98	.99	.006	.01 [*]
	b) Leg	.98	.94	.006	.04 [*]
Mean Difference: Stimulus Type	Arm - Leg	0	.05*		

Table 9. Mean TDR, Accuracy, Confidence Intervals, and Mean Differences as a Function of Presentation Format and Stimulus Type for the Naming Tasks

* = mean difference is significant.

The simple repeated measures ANOVA for accuracy was also significant, suggesting that there were differences in the accuracy of the four conditions, F(3, 150) = 19.943, p < .001. The results show that for arm stimuli, participants were more accurate when responding to pictures, whereas for leg stimuli, participants were more accurate when responding to words (see Table 9 for confidence intervals and mean differences between conditions). Furthermore, there were no differences in accuracy between arm and leg stimuli when participants were responding to words, but for pictures, participants were more accurate when responding to arm stimuli. As such, these results show that there are differences in accuracy dependent upon stimulus type and presentation format, unless both arm and leg stimuli are presented in word format.

Given that the Loftus and Masson (1994) confidence intervals showed evidence of an interaction, a 2X2 repeated measures factorial ANOVA was also run to determine whether there was an interaction between stimulus type (arm versus leg) and presentation format (pictures versus words) in the naming tasks. Mean TDR and accuracy are shown in Table 9. For TDR, the results show a significant main effect for stimulus type, F(1,50) = 8.872, p = .004, and a main effect of presentation format, F(1,50) = 647.38, p < .001. The results demonstrated that the interaction was also significant, F(1,50) = 98.503, p < .001. The significant interaction shows that for words participants were faster at responding to leg stimuli compared to arm stimuli, whereas

for pictures participants were faster at responding to arm stimuli compared to leg stimuli. For accuracy, the results show a significant main effect for stimulus type, F(1,50) = 28.496, p < .001, and a main effect of presentation format, F(1,50) = 10.76, p = .002. The results demonstrated that the interaction was also significant, F(1,50) = 20.395, p < .001. The significant interaction shows that for arm stimuli participants were more accurate when responding to pictures, whereas for leg stimuli, participants were more accurate responding to words. *Hemispherectomy Participants Arm Stimuli Analysis*

For calculating mean TDR in the arm naming task only correct responses were used. Mean TDR and accuracy for the arm naming task are shown in Table 2. Like in the semantic generation analyses, the hemispherectomy participants showed an impairment on task performance if their mean TDR and accuracy scores fell beyond 2 SD from the control group. Comparisons between the hemispherectomy participants mean TDR and accuracy and the control participants are shown in Figure 14. For the arm naming task, S.M. was faster at naming words (M = 1536 msec) compared to pictures (M = 1916 msec), and was more accurate naming words (M = .96) compared to pictures (M = .80). When compared to control participants' mean TDR, S.M. was 5.68 SD slower than controls when generating a response to words, and was 5.9 SD slower than controls when generating a response to pictures. When compared to control participants' mean accuracy scores, S.M. was .8 SD less accurate than control participants' accuracy when generating a response to pictures.

J.H. was faster at generating a response to words (M = 1492 msec) compared to pictures (M = 1974 msec), and was more accurate naming words (M = .96) compared to pictures (M = .88). When compared to control participants' mean TDR, J.H. was 5.26 SD slower than controls when generating a response to words, and was 6.37 SD slower than controls when generating a response to pictures. When compared to control participants' mean accuracy scores, J.H. was .8 SD less accurate than control participants' accuracy when generating a response to words, and was 4.35 SD less accurate than control participants' accuracy when generating a response to pictures. As such, these results suggest that for words, both participants are impaired on TDR, but not accuracy. For picture stimuli, however, both individuals show an impairment on TDR and accuracy. Furthermore, these results show evidence of a speed accuracy tradeoff, whereby S.M. is faster when identifying picture stimuli than J.H., but was also less accurate.

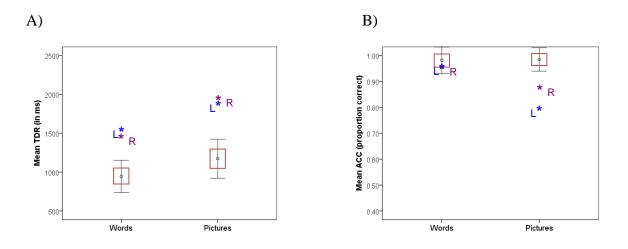


Figure 14. (A) Mean TDR (in milliseconds), and (B) Mean Accuracy (ACC, proportion correct) during the Arm Naming of Pictures and Words. L* has intact left hemisphere, *R has intact right hemisphere. Bar is ± 2 SD, box is ± 1 SD, around mean of normal controls.

Hemispherectomy Participants Leg Stimuli Analysis

For calculating mean TDR in the leg naming task only correct responses were used. Mean TDR and accuracy for the leg naming task are also shown in Table 2. Like in the arm naming analyses, the hemispherectomy participants showed an impairment on task performance if their mean TDR and accuracy scores fell beyond 2 SD from the control group. Comparisons between the hemispherectomy participants mean TDR and accuracy and the control group are shown in Figure 15. For the leg naming task, S.M. was faster at naming words (M = 1507 msec) compared to pictures (M = 2279 msec), and was also more accurate naming words (M = 1) compared to pictures (M = .50). When compared to participants' mean TDR, S.M. was 5.26 SD slower than controls when naming words, and was 6.5 SD slower than controls when naming pictures. When compared to control participants' mean accuracy scores, S.M. was 1 SD above control participants' accuracy when naming words, and was 7.46 SD less accurate than control participants' accuracy when naming pictures.

J.H. was faster at generating a response to words (M = 1609 msec) compared to pictures (M = 1905 msec)⁵, and was more accurate naming words (M = .95) compared to pictures (M =

⁵ It should be noted that in a recent review of the submitted manuscript version of this chapter (with the same data except for 2 stimuli), one reviewer raised a concern regarding how the TDR measure could be influenced by extreme (fast or slow) responses. To address this concern, the median TDR for the hemispherectomy participants was

.70). When compared to control participants' mean TDR, J.H. was 6.16 SD slower than controls when naming words, and was 4.13 SD slower than controls when naming pictures. When compared to control participants' mean accuracy scores, J.H. was .67 SD less accurate than control participants' accuracy when naming words, and was 4.07 SD less accurate than control participants' accuracy when naming pictures.⁶

compared to the mean of median TDRs for the control group. Median response times are less affected by extreme responses and thus were examined to control for variability in responses.

For the arm and leg picture and word semantic generation tasks, both J.H. and S.M. demonstrated some impairment compared to controls on median TDR. The median TDR for the arm picture and word semantic generation tasks show the same effects as the mean TDR analysis, while in the leg word condition, both individuals were now within 2 SD above controls' median TDR. Like the mean TDR analysis, it is only in the leg picture semantic generation task that a consistent impairment was shown across median TDR and accuracy.

For the arm and leg picture and word naming tasks, the analysis of median TDR show the same pattern of results as the analysis of mean TDR with the exception that both individuals perform similarly in the leg picture naming task on median TDR.

In addition, the same reviewer also requested that the hemispherectomy participants onset response times be compared the control groups' onset response times. Again, since medians are less affected by extreme responses, the hemispherectomy participants' median onset response times were compared to the mean median onset response times of the control group. In the arm semantic generation tasks, the comparison of median onset response times for the hemispherectomy participants showed the same patterns as the mean TDR comparison, with the exception that J.H. was within 2 SD of the controls' median onset response times for the hemispherectomy participants showed the exception that J.H. and S.M. only differed by 0.5 SD from one another for pictures. In the naming tasks, the comparisons of median onset response times for the hemispherectomy participants showed the same patterns as the mean TDR comparison that both individuals performed similarly on median onset response times in the leg picture naming task. Total duration to respond (and median TDR) represents how long it takes an individual to provide an object's use. Although two individuals may begin speaking at the same time, they may struggle in producing the use for an object, and thus TDR can be argued to be a more comprehensive measure of responding than onset response times. As such, it is treated as the preferred measure of response time in these analyses.

⁶ When the analysis was carried out with the 6 stimuli removed, the only consistent impairment (that is, across both response times and accuracy) for the hemispherectomy participants was, again, for leg picture stimuli. Thus with 6 stimuli removed, the hemispherectomy participants showed evidence of the same double dissociation that was shown in the analysis reported in the dissertation. When the analysis was carried out with no stimuli removed from the analysis, again the only consistent impairment found for the hemispherectomy participants was for leg picture stimuli. That is, with the inclusion of all stimuli, the individual with an intact right hemisphere (J.H.) demonstrated an impairment on response time for the semantic generation to leg pictures (6.02 SDs slower than the mean for controls and 3.68 SD slower than S.M.) and was 6.2 SD less accurate than the controls' mean accuracy, whereas the individual with an intact left hemisphere (S.M.) was 2.34 SD slower than control participants in this same condition and was 1.4 SD less accurate than the controls mean accuracy. For naming, the individual with an intact left hemisphere (S.M.) demonstrated an impairment in naming pictures of leg stimuli (5.49 SD slower than the mean for controls and almost 1.5 SD greater than J.H.) and 7.2 SD less accurate than the control participants' mean accuracy score (and more than 3 SD less accurate than J.H.), whereas the individual with an intact right hemisphere (J.H.) showed less impairment on TDR and accuracy. As such, the only difference in the results between the stimuli removed analysis (discussed in text) and no stimuli removed analysis, was that in the no stimuli removed analysis for the naming of leg picture stimuli, S.M. was closer to J.H.'s TDR (S.M. was alomost 1.5 SD slower than J.H.), but was even less accurate than J.H. (J.H. was 3.37 SD more accurate than S.M.).

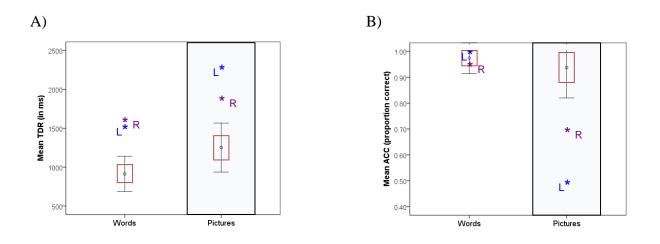


Figure 15. (A) Mean TDR (in milliseconds), and (B) Mean Accuracy (ACC, proportion correct) during the Leg Naming of Pictures and Words. L* has intact left hemisphere, *R has intact right hemisphere. Bar is ± 2 SD, box is ± 1 SD, around mean of normal controls.

Discussion

The results show that participants were faster when naming words compared to pictures. It was also shown that participants were more accurate naming leg words compared to leg pictures, but no differences were found for arm stimuli. The results also demonstrate differences in response times and accuracy dependent upon stimulus type. An examination of the hemispherectomy participants demonstrated that the most consistent finding (across both response time and accuracy) was that the individual with an intact left hemisphere (S.M.) demonstrated a severe impairment on accuracy and an impairment on TDR in naming pictures of leg stimuli, whereas the individual with an intact right hemisphere (J.H.) showed less impairment on TDR and accuracy. As such, there is a single dissociation present in the naming of leg picture stimuli.

Chapter 4 General Discussion

Performance on the Semantic Generation and Naming Tasks in Controls

Performance of Control Participants in the Semantic Generation Tasks (Experiments 4 and 5) for Arm and Leg Stimuli. The results from the semantic generation to arm stimuli showed only marginal differences in response times between picture and word stimuli. However, when a more powerful examination of the mean differences was carried out using the Loftus and Masson (1994) confidence intervals, the results showed that participants were significantly faster at responding to pictures compared to words. An examination of accuracy using these three analysis methods showed that there were no differences in accuracy between pictures and words. The same analyses were carried out for the leg semantic generation task and showed the same effects as those found for arm stimuli. That is, participants were faster at responding to pictures compared to words, but there were no differences in accuracy between pictures and words. Together, these results demonstrate that in the semantic generation tasks, participants are faster at generating a use for pictures compared to words, but there are no differences in how accurate participants are when responding to pictures and words.

A Comparison of the Performance of Control Participants in the Semantic Generation Tasks (Experiments 4 and 5) for Arm versus Leg Stimuli. A comparison of differences in response times and accuracy between the arm and leg semantic generation experiments was also carried out. The simple repeated measures ANOVA for TDR was significant, indicating that there is at least one significant difference between mean response times dependent upon presentation format and stimulus type. An examination of the mean differences in response times using the confidence intervals showed that participants were significantly faster responding to picture stimuli compared to word stimuli, regardless of stimulus type (arm versus leg). For both the semantic generation to pictures and words, there were no differences between response times for arm and leg stimuli. These results provide evidence that regardless of stimulus type (arm versus leg), when a person is providing a use for an object, they can access action-related semantic information faster when the stimulus is presented in picture format. For accuracy, the simple repeated measures ANOVA was not significant, but an examination of the mean differences in accuracy between arm and leg stimuli using the confidence intervals showed some significant differences. Specifically, the results showed that there were no differences in accuracy between pictures and words for arm and leg stimuli. However, when arm and leg

stimuli were presented in the same presentation format, participants were more accurate responding to arm stimuli than leg stimuli. As such, the analysis of accuracy suggests that regardless of the presentation format of the stimulus, participants were more accurate when responding to arm stimuli compared to leg stimuli. Taken together these results suggest that that although presentation format affects how quickly a participant responds to a stimulus, it does not affect the accuracy of the response. Instead, the stimulus type affects accuracy when responding in the semantic generation tasks, whereby regardless of presentation format, participants produced more accurate responses to arm stimuli.

Performance of Control Participants in the Naming Tasks (Experiment 6) for Arm and Leg Stimuli. The same analysis techniques as described above were used to examine the naming of arm stimuli and demonstrated that words were responded to significantly faster than pictures, but there were no differences in accuracy. An analysis of the naming of leg stimuli using these same measures demonstrated that participants were significantly faster and more accurate when responding to word stimuli compared to picture stimuli. Thus these results show that for arm and leg stimuli, the presentation format of the stimulus affects how quickly an individual is able to respond, with words being identified faster than pictures. Furthermore, for leg stimuli, the presentation format also affects how accurate an individual is when responding, whereby words are identified more accurately than pictures.

A Comparison of the Performance of Control Participants in the Naming Tasks (Experiments 6) for Arm versus Leg Stimuli. A comparison of differences in response times and accuracy between the naming tasks dependent upon stimulus type and presentation format was also carried out. The simple repeated measures ANOVA indicated that there was at least one significant difference in the TDR between the four conditions. An examination of mean differences between the tasks showed that across stimulus type (arm and leg) participants were faster to identify words compared to pictures. Moreover, the 2X2 factorial ANOVA and the confidence interval analysis showed an interaction between stimulus type and presentation format on TDR. Specifically, participants were faster at identifying leg word stimuli compared to arm word stimuli, but were faster identifying arm picture stimuli compared leg picture stimuli. As such, these results indicate that participants were faster at responding to word stimuli compared to picture stimuli regardless of the stimulus type (arm versus leg). Furthermore, the results demonstrated that there were differences in accuracy dependent upon stimulus type and

presentation format. For accuracy, the simple repeated measures ANOVA showed significant differences in accuracy between the four conditions. Again, an interaction was found between stimulus type and presentation format. Specifically, the results show that for arm stimuli participants are more accurate when responding to pictures, whereas for leg stimuli, participants were more accurate when responding to words. In addition, for word naming, there were no differences in accuracy dependent upon stimulus type; however, for picture naming, participants were more accurate identifying arm stimuli compared to leg stimuli. Together, these results show no differences in accuracy for words dependent upon stimulus type, but show that for pictures there were differences dependent upon stimulus type; and furthermore, show an interaction between presentation format and stimulus type for accuracy.

Differential Access to Action-Related Semantic Information.

Effect of Presentation format. Previous behavioural research has shown evidence that the presentation format of a stimulus affects an individual's ability to access different types of semantic information. Specifically, such research has shown that although both pictures and words have access to common action-related knowledge, stimuli presented in picture format have privileged access to action-related semantic information (Chainey & Humphreys, 2002; Saffran et al., 2003; Thompson-Schill et al., 2006), whereas words have more privileged access to word-associated knowledge (Chainey & Humphreys). As such, one goal of Chapter 4 was to examine whether there are differences in responding (both in terms accuracy and response times) in the semantic generation and naming tasks dependent upon the presentation format of the stimulus. To examine this, comparisons between responding to pictures and words in a task that targets action-related semantic information (i.e., the semantic generation tasks) and a task that does not target action-related semantic information (i.e., the naming tasks) were carried out.

In the semantic generation to both arm and leg stimuli, the results showed that participants could provide a use to pictures and words, demonstrating that both pictures and words have access to action-related semantic information. However, participants were faster at generating a use for pictures compared to words. There were no differences in participants' accuracy for pictures and words in the semantic generation task. The opposite effect was found in the naming tasks. Specifically, participants were faster identifying words compared to identifying pictures. Furthermore, there were differences found between pictures and words on accuracy. In particular, the results show that for arm stimuli there were no differences in

accuracy between pictures and words, but for leg stimuli, participants were more accurate when responding to words compared to pictures. As such, these results show that pictures have privileged access to action-related information (as shown by faster response times for pictures in the semantic generation tasks), whereas words have privileged access to word-associated information (as shown by faster response times for words in the naming tasks). Furthermore, these results show that differences in responding dependent upon presentation format are affected by task demands. Specifically, when a task targets action-related semantic information, as is the case in the semantic generation tasks, participants are faster at producing a response to pictures. However, in a task that does not target action-related semantic information, participants are faster at producing a response to words.

Effect of Stimuli Type. The behavioural examination of the semantic generation and naming tasks demonstrated that not only do pictures and words show differential access to semantic information, so to do arm and leg stimuli. Specifically, in the semantic generation tasks, there were no differences in response times for arm and leg stimuli, but show that participants were more accurate responding to arm stimuli compared to leg stimuli. For the naming tasks, an interaction between stimulus type and presentation format was found for response times and accuracy. Specifically, for words, participants were faster at naming leg stimuli, but for pictures, participants were faster at naming arm stimuli. With respect to accuracy, there were no differences in accuracy for naming arm and leg words, while for pictures participants were more accurate naming arm stimuli. Furthermore, for arm stimuli participants were more accurate naming pictures, while for leg stimuli participants were more accurate naming words. As such, these results demonstrate that arm and leg stimuli show differential access to action-related semantic representations dependent upon task complexity and presentation format. In the more complex semantic generation task, participants were more accurate generating responses to arm stimuli, suggesting that arms have more salient action programs than legs. In the naming task, participants took longer when responding to pictures suggesting that naming pictures is a more difficult task than naming words. Interestingly, no differences were found in accuracy during word naming for arm and leg stimuli, but participants were more accurate naming arm pictures compared to leg pictures. Thus the naming results suggests that when the task is more complex (naming pictures), participants show better performance when responding to arm stimuli compared to leg stimuli. Moreover, for leg stimuli participants showed better performance

naming words compared to pictures. The results suggest that leg stimuli are more difficult to name than arm stimuli, and furthermore, that when the stimulus is more difficult to name participants show better performance responding to words (which are easier to name than pictures). Together, these results suggest that arm stimuli may have more privileged access to semantic information in general compared to leg stimuli.

Responding to Action-Related Stimuli Post Right versus Left Hemispherectomy

J.H. (intact right hemisphere) and S.M. (intact left hemisphere) provided the first examination and comparison of how picture and word action-related semantic information is processed in an individual after the removal of an entire left or right hemisphere. The results demonstrate that both individuals showed some degree of impairment on the semantic generation (Experiment 4 and 5) and naming (Experiment 6) tasks. An examination of Figures 13, 15, and 16 revealed two dissociations that could be considered as consistent in terms of: (1) showing impairments on both response time and accuracy (i.e., if response time is slower than normal limits of the control participants, then accuracy should also be lower than normal limits of the controls), and (2) not showing a speed-accuracy tradeoff between the performance of each hemispherectomy individual (i.e., the individual who is slowest on TDR, to be impaired on that task, should also be lower on accuracy than the other individual). The most consistent effects (i.e., applicable across both response time and accuracy, and not involving any speed-accuracy tradeoffs) are the opposing single dissociations involving the leg picture stimuli. Specifically, in the semantic generation task, the individual with an intact right hemisphere (J.H.) demonstrated an impairment on response time for the semantic generation to leg pictures (6.18 SDs slower than the mean for controls and almost 2.5 SD slower than S.M.) and was 4.62 SD less accurate than the controls' mean accuracy, whereas the individual with an intact left hemisphere (S.M.) was less than 4 SD from the mean of control participants in this same condition, and was .77 SD less accurate than the controls mean accuracy. In the naming task, the opposite single dissociation was found. Specifically, the individual with an intact left hemisphere (S.M.) demonstrated an impairment in naming pictures of leg stimuli, whereby she was 6.5 SD slower than the control participants' mean TDR (and almost 2.5 SD slower than J.H.) and 7.46 SD less accurate than the control participants' mean accuracy score (and more than 3 SD less accurate than J.H.), whereas the individual with an intact right hemisphere (J.H.) showed less impairment

on TDR and accuracy. As such, the two opposing single dissociations provide evidence of a double dissociation (see Figure 16 for a side-by-side comparison of the double dissociation).

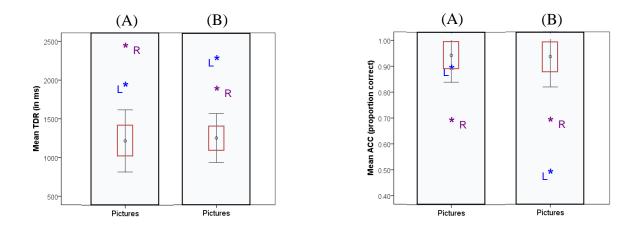


Figure 16. The Double Dissociation found between Task and Intact Hemisphere for Leg Picture Stimuli. A) The semantic generation to leg pictures; B) The naming of leg pictures.

Previous neuroimaging research has provided evidence as to which brain regions are involved in the processing of semantic knowledge. Specifically, functional neuroimaging research has shown that a left dominant network of brain regions are activated during the processing of semantic information (e.g., Martin, 2007; Martin, 2001; Martin et al., 1995; 1996; Martin and Chao, 2001; Thompson-Schill, 2003; Thompson-Schill et al., 2006), with damage to the left hemisphere being shown to interfere with the retrieval of semantic knowledge (Hart & Gordon, 1990). In addition, the processing of action-related embodied language has been shown to be a left-dominant process, in that responding to action-related stimuli produces activation in the left PFN (Esopenko et al., 2008; Hauk et al., 2004; Tettamanti et al., 2005; Aziz-Zadeh et al., 2006a). As shown in Chapter 3, when participants verbalize how they would interact with actionrelated stimuli, arm stimuli are processed bilaterally for both picture and word formats, whereas regardless of presentation format, leg stimuli show left hemisphere dominant processing. Based on this research, it was predicted that the individual with an intact left hemisphere would show better overall performance (more correct responses and faster response times) on both the naming and semantic generation tasks and specifically with leg stimuli. However, the double dissociation between intact hemisphere and task performance with leg picture stimuli suggests

that this is not quite the case, given that the participant with the intact left hemisphere is impaired compared to the individual with the intact right hemisphere on naming leg picture stimuli. Together, these results provide insight as to which hemispheres are necessary to perform the tasks.

Necessity of the Right and Left Hemisphere when Responding to Action-related Stimuli

Price et al. (2006) have suggested that neuroimaging research on normal participants can show us what regions might be sufficient for processing a specific task or function, whereas the necessity of a brain region to perform a task can only be determined when damage to a region results in a loss of function or an inability to perform a task correctly (or within normal limits). As such, it was proposed that examining the processing of action-related stimuli in an individual post-left or post-right hemispherectomy should help provide an understanding of the necessity of the left or the right hemisphere for the processing of such stimuli. The fMRI results shown in Chapter 3 demonstrated bilateral activation in the PFN regardless of stimulus format (i.e., pictures and words) for arm stimuli, and left dominant activation in the PFN regardless of stimulus format for leg stimuli, thus suggesting that these regions are sufficient for responding to action-related language. Examining J.H.'s and S.M.'s performance on the picture and word naming and semantic generation tasks allowed for the evaluation of the necessity of each hemisphere in processing action-related stimuli. The results showed that, specifically for leg picture stimuli, the right hemisphere seems to be more critical for naming, while the left hemisphere seems to be more critical for naming, while the left

The dissociation only occurring for leg stimuli and not arm stimuli can perhaps be best understood in light of semantic generation to leg stimuli having been shown to be a left dominant process, whereas arm stimuli are shown to be processed bilaterally (see Chapter 2 and 3; Hauk et al., 2004). Interestingly, a recent study Arevalo and colleagues (in press) found that patients who had a stroke resulting in damage to Brodmann's area 4/6 (primary motor and premotor cortices) were less accurate responding to leg-related stimuli. Specifically, on an action-related picture and word matching task, patients were less accurate when responding to leg-related stimuli than leg neutral stimuli, but did not differ on accuracy for mouth-related versus mouth neutral and handrelated versus hand neutral stimuli. This finding may be due to foot items being "less salient" (pg. 7), and thus more affected by a lesion to the motor regions. As such, it could be argued that since leg stimuli are believed to be less salient, it could make responding to leg stimuli more

difficult. The results from the two hemispherectomy participants support this, and show that the task with higher semantic demands (semantic generation to leg stimuli) elicited better performance from the participant with the intact left hemisphere. However, the question remains as to why this same participant performed more poorly than the participant with the intact right hemisphere in the naming of the same stimuli. Previous research examining language function post-right and post-left hemispherectomy has shown that if damage occurs in childhood, then language functions should be reorganized in the healthy hemisphere (Liegeois et al., 2004; Liegeois, Connelly, Baldeweg, Vargha-Khadam, 2008), and furthermore, that the right hemisphere can take on language functions, but only if damage occurs early in childhood (Liegeois et al., 2008). S.M. (intact left hemisphere) began experiencing seizures at age 5 and a left-sided hemiparesis at age 6, while J.H. (intact right hemisphere) was noted to have a rightsided hemiparesis shortly after birth, and at age 8, began experiencing simple partial motor seizures that progressed into generalized tonic-clonic seizures. Given that hemiparesis was noted early in childhood, it can be assumed that damage to the affected hemispheres occurred early for both individuals. As such, it could be the case that when a task requires less semantic knowledge (such as in naming), the right hemisphere is capable of completing the task because basic language functions have transferred to the right hemisphere. However, when the task is more difficult, it requires greater demands, which the right hemisphere may not be capable of because this information may not have transferred over. Hence, when the task requires greater semantic demands (such as in semantic generation), the left hemisphere is more able to perform the task because of its greater language capacity. Thus, when the task requires less semantic involvement, the individual with the intact right hemisphere performs well, whereas when the task requires greater semantic involvement, the individual with the intact left hemisphere performs well. However, a question for future research remains: why does the individual with an intact left hemisphere perform poorer at a task that requires less semantic involvement?

Conclusion

The results from Experiments 4-6 are consistent with previous research showing that the presentation format of the stimulus affects responding. Specifically, these results suggest that pictures have privileged access to action-related semantic knowledge, while words may have privileged access to word-associated knowledge. In addition, an examination of the hemispherectomy participants' performance in the semantic generation and naming tasks

demonstrated that the only consistent impairment, across both response times and accuracy with no evidence of a speed accuracy tradeoff, was for leg picture stimuli. Furthermore, the results from the hemispherectomy participants provide evidence of a double dissociation between task and intact hemisphere for leg-related picture stimuli. Finally, the results for the hemispherectomy participants provide novel evidence regarding the necessity of the right and left hemispheres for the naming and semantic generation of leg-related picture stimuli, respectively.

CHAPTER 5

EXAMINING THE EFFECT OF EFFECTOR: THE RELATIONSHIP BETWEEN BODY-OBJECT INTERACTION RATINGS, INCONGRUENT VERSUS CONGRUENT EFFECTOR RESPONSE, AND LIMB DOMINANCE

As discussed earlier, previous behavioural research has provided support for the theory of embodied cognition, whereby language comprehension has been shown to be grounded in bodily interaction. Furthermore, previous research has shown that the degree of embodiment of a word affects responding. Specifically, Siakaluk and colleagues (2008a; 2008b) have shown that words rated as higher in BOI (or easier to physically interact with), have a greater amount of sensorimotor knowledge associated with them, and are thus responded to more quickly and accurately in variants of the lexical decision and semantic categorization tasks. However, words rated as lower in BOI (or more difficult to physically interact with), have less sensorimotor knowledge associated with them, and are thus responded to more slowly and less accurately. These findings suggest that the degree of embodiment of a stimulus, affects semantic processing.

Previous behavioural research has also shown that when participants have to make a motor response to a sentence implying an action, facilitation in responding is shown when the response action is congruent with the action implied of the sentence (Glenburg & Kaschak, 2002). In their experiment, Glenberg and Kaschak had participants judge the sensibility of sentences that implied a direction either away from the body or toward the body. Participants were required to make sensibility judgments by pressing a 'yes' or 'no' button with their dominant hand, whereby the 'yes' or 'no' buttons were either near or far from their body. The authors found that participants were faster at responding when the response action and implied sentence action were congruent, whereas interference was shown when the response action was incongruent with the implied action of the sentence. This relationship has been referred to as the action-compatibility effect (Glenberg & Kaschak). Interestingly, Scorolli & Borghi (2007) examined whether language is grounded in sensorimotor processing by having participants respond using different effectors (e.g., arm versus leg). In this experiment, participants were presented with verb and noun pairs referring to mouth actions (e.g., "to suck the sweet"), hand actions (e.g., "to unwrap the sweet") and foot actions ("to kick the ball"), and participants had to decide whether the combination of the noun and verb made sense. Scorolli

and Borghi compared the processing of mouth action pairs to hand action pairs, and also the processing of foot action pairs to hand action pairs. For the mouth-hand comparison, participants responded yes into a microphone if the pair made sense, while for the foot-hand comparison, participants responded by pressing a foot pedal with their right foot if the pair made sense. The authors predicted that if language is grounded in sensorimotor processing, then participants should be faster at deciding if the verb-noun pair made sense if the implied action of the sentence was congruent with the effector making the response. Thus, in the mouth-hand comparison, participants should be faster responding into the microphone for mouth sentences compared to hand sentences, whereas for the foot-hand comparison, participants should be faster at pressing a pedal with their foot for foot sentences compared to hand sentences. The authors found that when responding into a microphone, participants were faster at making a decision to mouth sentences compared to hand sentences, whereas for the pedal response, participants were faster at responding to foot sentences compared to hand sentences. These results provide support for the theory of embodied cognition, in that they show that language processing is grounded in bodily interaction.

Summary and Hypotheses

Previous behavioural research has shown BOI ratings to be a good measure of the degree of embodiment associated with a word. That is, words that are rated as higher in BOI have been shown to be responded to more quickly than words rated as lower in BOI. In addition, previous research has shown that language comprehension is grounded in sensorimotor processing, whereby the action implied by a sentence affects the speed of a physical response to the sentence. Specifically, when the action implied by the sentence was congruent with the response effector, participants were faster to respond, whereas when the action implied by the sentence was incongruent with responding, participants were slower to respond. However, previous research has not examined: (1) whether a BOI advantage for reaction times and accuracy is shown when the stimulus type (arm and leg) and effector (arm and leg) are congruent or incongruent; and (2) whether a BOI advantage for reaction times and accuracy is shown when participants respond with their dominant versus non-dominant effectors; (3) how an effectorspecific response (having participants respond with their arm versus leg) affects responding in a semantic categorization task (categorizing whether the object is used by the arm or leg); and (4) whether responding with the dominant versus non-dominant hand or foot affects responding in a semantic categorization task.

To examine this, Chapter 5 consists of two experiments. In Experiment 7, participants were required to categorize whether a word refers to an object that is used by the arm or leg by responding with their dominant hand and foot. In Experiment 8, participants were required to categorize whether a word refers to an object that is used by the arm or leg by responding with their non-dominant hand and foot. BOI ratings were also collected to determine whether words rated as higher in BOI were responded to more quickly when responding with the hand or foot effector. One goal of these experiments was to collect BOI ratings on a new set of stimuli developed for these experiments, and to determine whether a BOI advantage (faster responding to words rated as higher in BOI) was shown when participants responded with their hand or foot. The second goal of these experiments was to determine how the response effector affected responding in a semantic categorization task using the dominant (Experiment 7) and nondominant (Experiment 8) effectors. Specifically, will participants respond more quickly when the effector response and stimulus type are congruent, and furthermore, will a congruency effect be shown when responding with the dominant and non-dominant effectors? Based on the research described above, it was hypothesized that: (1) words that are rated as higher in BOI will be responded to faster regardless of whether the response effector and stimulus type are congruent or incongruent, and when the dominant or non-dominant effector is used to respond; (2) participants would respond faster to arm and leg stimuli when the response effector (hand or foot) and stimulus type (arm or leg) were congruent (e.g., when the foot responded to foot/leg stimuli and when hand responded to hand/arm stimuli), compared to when the effector response and stimulus type are incongruent (e.g., when the hand responded to leg stimuli and when foot responded to arm stimuli); and (3) the congruency effect should occur regardless of whether participants respond with their dominant versus non-dominant effectors.

Experiment 7

The goal of Experiment 7 was to examine whether words rated as higher in BOI are responded to more quickly, and moreover, to examine how the congruence or incongruence of the dominant response effector affects responding in a semantic categorization task.

Materials and Methods

Participants

Undergraduate university students (N = 40; mean age = 20.1) with normal or corrected to normal vision participated in the following experiment for course credit in their introductory psychology class. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences Ethics Committee.

Stimuli and Procedure

Stimuli consisted of 48 arm stimuli and 48 leg stimuli (see Appendix B, which contains 48 stimuli of the arm type and 48 stimuli of the leg type; two additional items of each type had been included, but were removed from the analyses due to unusual spellings (three items) or lack of BOI rating (1 item)).

Participants first completed a handedness and footedness questionnaire to determine their dominant limb (Appendix C; Elias, Bryden, & Bulman-Flemming, 1998). Participants then completed a semantic categorization task. In this task, words referring to items used by the arm or leg were presented on a screen (IBM E94 monitor) using EPrime programming software. Participants were instructed to categorize the words as used by either the arm or leg when the word was presented on the screen. Words remained on the screen until participants completed a response. Participants responded using two pedals that were interfaced with the Eprime serial response box, one with their dominant hand and one with their dominant foot. In one block, participants responded to half of the stimuli, whereby they responded to hand/arm stimuli using their hand, and to foot/leg stimuli using their foot. In the second block, participants responded to half of the stimuli using their foot, and to foot/leg stimuli using their foot. Response times and accuracy rates were counterbalanced across participants. Response times and accuracy rates were collected.

After completing the semantic categorization task, participants completed BOI ratings of the same words that they had responded to in the semantic categorization task. Words were

presented on the monitor, and participants were instructed to indicate the ease or difficulty with which the human body can physically interact with the word's referent on a scale of 1 (item is difficult to interact with) to 7 (item is easy to interact with). Participants typed responses into a keyboard. One participant's BOI ratings were not included in the following BOI analyses because the experimenter noticed they appeared to be using the rating scale for BOI in the opposite direction than instructed.

Results

Given that one goal of this experiment is to examine the relationships between reaction times (RT) and accuracy with BOI, which is an item-based characteristic, the analyses carried out in this chapter are based on items as the unit of analysis (a by-item analysis). Six participants were not included in the analyses due to having mixed dominance (e.g., dominant foot = left, dominant arm = right, or vice versa).

The Relationship between RT, Accuracy, BOI Ratings, and Effector

For calculating mean RT only correct responses were used, and if an item's mean RT or accuracy was greater than \pm 3 SD from the mean, the item was not included in the RT and accuracy BOI correlation analyses. The same outlier procedure was used for all conditions and resulted in 2 items not being included in the analysis of arm stimuli responded to with the hand effector; two items not being included in the analysis of arm stimuli responded to with the foot effector; two items not being included in the analyses leg stimuli responded to with the foot effector; and 1 item not being included in the analyses leg stimuli responded to with the hand effector.

Arm Stimuli Responded to with the Hand Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r(45) = -.387, p = .008. A correlation analysis between accuracy and BOI ratings also showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more accurately, r(45) = .297, p = .045.

Arm Stimuli Responded to with the Foot Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r (45) = -.387, p = .008. A correlation analysis between accuracy and BOI ratings also showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more accurately, r (45) = .347, p = .018.

Leg Stimuli Responded to with the Foot Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r(45) = -.347, p = .018. A correlation analysis between accuracy and BOI ratings was not significant, r(45) = .047, p = .754.

Leg Stimuli Responded to with the Hand Effector. No significant relationships were found between RT and BOI, r(46) = -.241, p = .103, and between accuracy and BOI, r(46) = .097, p = .515.

Reaction Times and Accuracy Rates

The same outlier technique as described above was used and resulted in 3 items not being included in the RT and accuracy analyses for arm stimuli; two items not being included in the RT and accuracy analyses for leg stimuli; and 5 items not being included in the within-effector, between stimuli, ANOVA analysis.

Responding to Arm Stimuli with the Dominant Effector. A paired comparison t-test shows a congruency effect, whereby participants were significantly faster responding to arm stimuli when responding with the hand effector (M = 1066.73 msec), compared to the foot effector (M = 1130.20 msec), t (44) = -3.190, p = .003. Furthermore, participants were significantly more accurate responding to arm stimuli with their hand effector (M = .96), compared to the foot effector (M = .93), t (44) = 2.618, p = .012.

Responding to Leg Stimuli with the Dominant Effector. A paired comparison t-test showed that participants were marginally faster at responding to leg stimuli with their hand effector (M = 1098.69 msec), compared to the foot effector (M = 1137.93 msec), however, this comparison was not significant, t (45) = -1.568, p = .124. Furthermore, a paired comparison t-test of accuracy rates showed that there was no significant difference in accuracy when participants responded to leg stimuli with their hand effector (M = .96), t (45) = .023, p = .982.

Given that the paired t-tests suggested evidence for a congruency advantage when responding with the hand, but not with the foot, an ANOVA with effectors as a within-item factor, and stimulus type as a between-item factor was conducted to examine whether there were differences in responding to hand/arm and foot/leg stimuli within-effectors. The RT analysis demonstrated a significant main effect of effector (hand versus foot), F(1,89) = 10.721, p = .002, but no significant main effect of stimulus type (hand/arm versus foot/leg), F(1,89) = .331, p =

.567. The interaction between effector and stimulus type was not significant, F(1,89) = .572, p = .452. The accuracy analysis demonstrated a marginal main effect of effector, F(1,89) = 3.843, p = .053, and the main effect of stimulus type was not significant, F(1,89) = .515, p = .475. A marginal interaction between effector and stimulus type was also found, F(1,89) = 3.725, p = .057. The RT and accuracy analyses demonstrate that there are differences in how hand/arm and foot/leg stimuli were responded to dependent upon effector.

Together, the paired t-tests suggest a congruency advantage when responding to hand/arm stimuli with the hand, and a congruency disadvantage responding to foot/leg stimuli with the foot. However, given that the within effector ANOVA demonstrated a main effect of effector, this suggests that the congruency advantage for the hand effector, and the congruency disadvantage for the foot effector, could be due to hands being faster to respond in this task. Thus, to examine whether these effects could be due to the hands being faster for responding than feet in this task, by-subject paired comparison t-tests were carried out to determine if there were differences in responding to hand/arm and foot/leg stimuli within-effectors. *Examining Congruency within Effectors*

For calculating by-subject mean RT, only correct responses were used, and if a participant's mean RT or accuracy was greater than ± 3 SD from the mean, the participant was not included in the RT and accuracy analyses. For the within-hand effector analysis, this resulted in 2 participants not being included in the RT and accuracy analysis, and no participants being excluded in the within-foot effector analysis.

Responding to Arm and Leg Stimuli with the Dominant Hand Effector. The by-subject paired t-test indicated that there were no differences in how quickly the hand responded to hand/arm (M = 1048 msec) and foot/leg (M = 1076 msec) stimuli, t (31) = -1.164, p= .253. The by-subject analysis of accuracy demonstrated that there were no significant differences in accuracy between hand/arm (M = .95) and foot/leg (M = .95) stimuli when responding with the hand, t (31) = -.027, p = .978. These results show that there were no within-effector congruency effects for RT or accuracy when responding to hand/arm and foot/leg stimuli. As such, these results indicate that the congruency advantage shown in the earlier by-item analysis when responding with the hand may be due to hand being a faster effector in general.

Responding to Arm and Leg Stimuli with the Dominant Foot Effector. The by-subject paired t-test for RT demonstrated that there were no significant differences in how fast the foot

responded to hand/arm (M = 1139 msec) and foot/leg (M = 1164 msec) stimuli, t (33) = -.798, p = .430. The by-subject paired t-test for accuracy demonstrated that there were no significant differences in accuracy between hand/arm (M = .92) and foot/leg (M = .93) stimuli when responding with the foot, t (33) = -.797, p = .431. These results show that there were no within-effector differences for RT or accuracy when responding to hand/arm and foot/leg stimuli. This suggests that the congruency disadvantage shown when responding with the foot may be due to foot being slower to respond in this task compared to the hand.

Discussion

An examination of the relationship between RT and BOI, and accuracy and BOI, showed that for hand/arm stimuli words rated as higher in BOI were responded to more quickly and accurately than words rated as lower in BOI, regardless of whether participants responded with their dominant hand or dominant foot. For foot/leg stimuli, however, words rated as higher in BOI were responded to more quickly than words rated as lower in BOI, but only when participants responded with their dominant foot. An examination of reaction times and accuracy when participants responded with their dominant effector demonstrated a significant congruency advantage for hand/arm stimuli. Conversely, for foot/leg stimuli, there were no significant differences in response times and accuracy when participants responded with their dominant foot. A discussion of these results, and explanations for why differences were shown dependent upon stimulus type, will occur in more detail in the General Discussion for Chapter 5.

Experiment 8

The goal of Experiment 8 was to examine whether words rated as higher in BOI are responded to more quickly, and furthermore, to examine how the congruence or incongruence of the non-dominant response effector affects responding in a semantic categorization task. In addition, having participants respond to the same stimuli using their non-dominant effectors will allow for a within-effector analysis of congruency, so as to again address whether the congruency advantage shown for hands in Experiment 7 is driven by an arm-effector advantage when responding with the non-dominant effector.

Materials and Methods

Participants

A separate group of undergraduate university students (N = 40; mean age = 20.2) with normal or corrected to normal vision participated in the following experiment for course credit in their introductory psychology class. The research was performed in compliance with the Helsinki Declaration of 1983, and was approved by the University of Saskatchewan Behavioural Sciences Ethics Committee.

Stimuli and Procedure

The stimuli and procedure are the same as those used in Experiment 7, with the exception that participants responded with their non-dominant effector. One participant's BOI ratings were not included in the following BOI analyses because the experimenter noticed they appeared to be using the rating scale for BOI in the opposite direction than instructed.

Results

As in Experiment 7, by-item analyses were used to examine RT, accuracy, and their relationship with BOI. Seven participants were not included in the analysis due to having mixed dominance (dominant foot = left, dominant arm = right, or vice versa).

The Relationship between RT, Accuracy, BOI Ratings, and Effector Response

The same outlier procedure as in Experiment 7 was used for all conditions and resulted in 2 items not being included in the analysis of arm stimuli responded to with the hand effector; one item not being included in the analysis of arm stimuli responded to with the foot effector; two items not being included in the analyses leg stimuli responded to with the foot effector; and 2 items not being included in the analyses leg stimuli responded to with the hand effector.

Arm Stimuli Responded to with the Hand Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r(45) = -.350, p = .017. A correlation analysis between accuracy and BOI ratings was not significant, r(45) = .192, p = .202.

Arm Stimuli Responded to with the Foot Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r(46) = -.299, p = .041. A correlation analysis between accuracy and BOI ratings was not significant, r(46) = .187, p = .207.

Leg Stimuli Responded to with the Leg Effector. A correlation analysis between RT and BOI ratings showed a significant BOI advantage, whereby words rated as higher in BOI were responded to more quickly, r (45) = -.300, p = .043. A correlation analysis between accuracy and BOI ratings was not significant, r (45) = -.096, p = .524.

Leg Stimuli Responded to with the Hand Effector. No significant relationships were found between RT and BOI, r(45) = -.159, p = .291, and between accuracy and BOI, r(45) = -.006, p.968.

Reaction Times and Accuracy Rates

The same outlier technique as in Experiment was used and resulted in 2 items not being included in the RT and accuracy analyses for arm stimuli; three items not being included in the RT and accuracy analyses for leg stimuli; and 5 items not being included in the within-effector, between stimuli, ANOVA analysis.

Responding to Arm Stimuli with the Non-Dominant Effector. A paired comparison t-test shows a congruency effect for arm stimuli, whereby participants were significantly faster responding to arm stimuli when responding with the hand effector (M = 993.48 msec), compared to the foot effector (M = 1240.96 msec), t (44) = -8.989, p < .001. There was no significant difference in accuracy when participants responded to arm stimuli with their hand effector (M = .96), compared to the foot effector (M = .94), t (45) = 1.486, p = .144.

Responding to Leg Stimuli with the Non-Dominant Effector. A paired comparison t-test showed that participants were significantly faster responding at responding to leg stimuli with their hand effector (M = 981.10 msec), compared to the foot effector (M = 1199.52 msec), t (44) = -10.429, p < .001. Furthermore, a paired comparison t-test of accuracy rates showed that

participants were more accurate responding to leg stimuli with their hand effector (M = .94), compared to the foot effector (M = .90), t (44) = 3.175, p = .003.

Like in Experiment 7, given that a congruency advantage was shown when responding with the hand and a congruency disadvantage was shown when responding with the foot, an ANOVA with effectors as a within-item factor, and stimulus type as a between-item factor was conducted to address whether there were differences in responding to hand/arm and foot/leg stimuli within-effectors. The RT analysis demonstrated a significant main effect of effector (hand versus foot), F(1,89) = 180.293, p < .001, but no significant main effect for stimulus type (hand/arm versus foot/leg), F(1,89) = .703, p = .404. The interaction between effector and stimulus type was not significant, F(1,89) = .701, p = .405. The accuracy analysis demonstrated a significant main effect of stimulus type was not significant, F(1,89) = 10.815, p = .001, and a significant main effect of stimulus type was not significant, F(1,89) = 1.386, p = .242. The RT and accuracy analyses demonstrate that there are differences in how hand/arm and foot/leg stimuli were responded to dependent upon effector.

Like Experiment 7, the paired t-tests suggest a congruency advantage when responding to hand/arm stimuli with the hand, and a congruency disadvantage responding to foot/leg stimuli with the foot. However, the results from the within-effector ANOVA demonstrate that the congruency advantage and disadvantage shown in these analyses may be again due to hands being faster to respond compared to feet. To examine this, the same by-subject paired comparison t-tests as in Experiment 7 were carried out.

Examining Congruency within Effectors

The same by-subject outlier technique as described in Experiment 7 was used and resulted in 2 participants not being included in the non-dominant hand effector analyses, and 2 participants not being included in the non-dominant foot effector analyses.

Responding to Arm and Leg Stimuli with the Non-Dominant Hand Effector. The bysubject paired t-test for RT demonstrated that there were no significant differences in how fast the hand responded to hand/arm (M = 943 msec) and foot/leg (M = 951 msec) stimuli, t (30) = -.389, p = .700. The by-subject paired t-test for accuracy demonstrated that participants were more accurate responding to hand/arm (M = .95) than foot/leg (M = .91) stimuli when responding with the hand, t (30) = 2.411, p = .022. As such, like Experiment 7, these results show that there were no within-effector differences in RT when responding to hand/arm and foot/leg stimuli.

Thus, it can be suggested that the congruency advantage for the hand effector shown in the earlier by-item analysis may be due to the hand being faster to respond to hand/arm stimuli in this task. However, the results do show that participants are more accurate responding with their hand to hand/arm stimuli compared to foot/leg stimuli.

Responding to Arm and Leg Stimuli with the Non-Dominant Foot Effector. The bysubject paired t-test for RT demonstrated that there were no significant differences in how fast the foot responded to hand/arm (M = 1171 msec) and foot/leg (M = 1162 msec) stimuli, t (30) = .239, p = .813. The by-subject t-test for accuracy demonstrated that there were no significant differences in accuracy between hand/arm (M = .94) and foot/leg (M = .93) stimuli when responding with the hand, t (30) = .384, p = .704. These results show that there were no withineffector differences in RT or accuracy when responding to hand/arm and foot/leg stimuli. As such, like Experiment 7, these results show that the congruency disadvantage for the foot effector may be due to the foot being slower to respond.

Discussion

The results from Experiment 8 (non-dominant effector) demonstrate a BOI advantage between RT and BOI for arm stimuli regardless of whether participants responded with their non-dominant hand or non-dominant foot. However, for foot/leg stimuli, a BOI advantage was only shown when participants responded with their non-dominant foot. The results from Experiment 8 also demonstrate a significant congruency advantage for hand/arm stimuli, and a congruency disadvantage for foot/leg stimuli. Like the results from Experiment 7, the withineffector analyses demonstrated that there were no differences in RT when responding to hand/arm and foot/leg stimuli with the non-dominant hand. However, when responding with the hand, participants were more accurate responding to hand/arm compared to foot/leg stimuli. Thus, while within-effector analyses suggests that the advantage found when responding with the non-dominant hand may be due to the hand being a faster effector than the foot, there still remains a significant congruency effect on accuracy. These results will be discussed in more detail in the General Discussion for Chapter 5.

Chapter 5 General Discussion

Relationship between Reaction Times, Accuracy and Body-Object Interaction in a Semantic Categorization Task

Previous research has shown that the sensorimotor information associated with a word (or its referent) affects the recognition of words. For example, Siakaluk and colleagues (2008a; 2008b) have shown that high BOI words are responded to more quickly and accurately in tasks that target phonological, orthographic and semantic information compared to low BOI words. The authors suggest that words rated higher in BOI have a greater amount of sensorimotor knowledge associated with them and activate richer action-related semantic representations, thus resulting in faster and more accurate responses. Words rated lower in BOI, on the other hand, have less sensorimotor knowledge associated with them, thus activating less rich action-semantic representations, resulting in slower and less accurate responses. However, the tasks examined by Siakaluk and colleagues did not involve having participants respond with their foot effector.

The results from Experiment 7 show that for hand/arm stimuli, when responding with the dominant hand and foot effectors, words rated as higher in BOI were responded to faster and more accurately than words rated as lower in BOI. However, for foot/leg stimuli, a BOI advantage was only shown when the stimulus type and response effector were congruent. That is, a BOI advantage was shown for leg words only when they were responded to with the dominant foot. The results from Experiment 8 show the same BOI effects on RT. Thus, although these results show a significant BOI advantage for arm and leg stimuli, they also demonstrate that the effector used to respond affects the relationship between RT and accuracy with BOI ratings.

One question that remains is: why do arm stimuli show a significant BOI advantage regardless of whether they are responded to with the hand or foot, whereas a significant BOI advantage is only shown for leg stimuli when they are responded to with the foot? One answer could be that the differences in the BOI advantages shown for arm and leg stimuli are due to arms having a more extensive action program than legs. That is, arm stimuli have been suggested to have a larger repertoire of action programs associated with them, resulting in arms having a richer network of sensorimotor representations than legs (Esopenko et al., 2008; Pulvermuller et al., 2005a). Leg stimuli, however, have been suggested to have less extensive action programs associated with them, resulting in a less rich network of sensorimotor representations (Esopenko et al., 2008; Pulvermuller et al., 2005a). Furthermore, given the more extensive action programs

and representation along the motor cortex for arms, then there should be no interference when simultaneously activating the action-related semantic representations for arm stimuli and the motor program for hands. However, given the less extensive action programs and representation along the motor cortex for legs, the simultaneous activation of the action-related semantic representations for leg stimuli and the motor programs for legs, should cause interference.

As such, given that arms activate a greater network of sensorimotor representations, which is extended when words are more embodied (or higher in BOI), high BOI words are responded to significantly faster regardless of whether arm stimuli are being responded to with the arm or leg. Conversely, although leg stimuli activate fewer sensorimotor representations, when leg stimuli are rated as higher in BOI, they should activate a richer network of sensorimotor representations than leg stimuli rated as lower in BOI. Given that responding with the foot to leg stimuli has been shown to cause interference resulting in slower responding (both shown in the RT analyses in Experiment 7 and 8, and similarly by Buccino et al., 2005, discussed below), stimuli that are or more embodied (or easier to interact with) produce a greater amount of sensorimotor representations than stimuli that are less embodied (or more difficult to interact with), thus decreasing the interference in responding caused by simultaneously activating the motor program for foot and action-related semantic representations for foot. That is, responding to words that are more embodied causes less interference when responding with the foot, resulting in faster response times. Since, there is no interference when responding with the hand to leg stimuli, the degree of embodiment of a stimulus does not affect responding to leg stimuli with the hand.

The neuroimaging results presented in Chapters 2 and 3 for the word semantic generation task may also provide insight into why differences in BOI effects were shown. Semantic generation to arm stimuli produced bilateral activation, whereas the semantic generation of leg stimuli mainly activated the left hemisphere. Thus, the neuroimaging results show that arm stimuli activate a more extensive, bilateral network of action-related semantic representations compared to leg stimuli. Given that language is thought to be grounded in sensorimotor processing, this would suggest that if stimuli activated a larger network of action-related semantic representations, then this should facilitate the processing of such stimuli. Thus given that arms activate a larger network of action-related semantic representations, then it could be predicted that the processing of arm stimuli would be faster. With this prediction in mind, the

BOI advantage shown for responses to arm stimuli, regardless of the effector used to respond, makes sense. That is, arm words that are more embodied activate a larger network of actionrelated semantic representations than arm words that are less embodied. Because words that are more embodied activate a more extensive network of sensorimotor representations, they can be responded to more quickly, even with the incongruent effector. Conversely, because leg words activate a more constrained network of action-related semantic representations, even leg words rated as more embodied activate fewer sensorimotor representations compared to arm words. However, the greater sensorimotor representations associated with high BOI words enables the foot to respond faster to high BOI words compared to low BOI words, whereas the hand effectors are able to respond quickly to leg words regardless of the degree of embodiment of the word. Thus the BOI advantage for leg words is only shown when responding with the congruent effector. As such, these results provide support for the idea that language is grounded in sensorimotor processing, but also show that the richness of the sensorimotor representations associated with a word affects how it will be responded to.

Response Times and Accuracy

Previous research has shown a congruency effect, wherein there is increased speed and accuracy of response, when the implied action of a sentence is congruent with the action required when making a response. For example, Glenburg & Kaschak (2002) showed facilitation in responding when the action implied in a sentence was congruent with the response action, whereas inference in responding was shown when the action implied in a sentence was incongruent with the response action. These results indicate that when a physical response is required, the implied action in the sentence affords an action and thus facilitates responding. Furthermore, previous research has shown that when the sentence action is congruent with the response effector, facilitation in responding occurs (Scorolli & Borghi, 2007). For example, when participants make a decision of whether a verb and noun make sense together, participants are faster to respond to mouth sentences compared to hand sentences when responding into a microphone, whereas participants are faster to respond to leg sentences compared to hand sentences when responding with a foot pedal. These results show that participants are able to make a faster decision when the implied action of a sentence is congruent with the response effector (e.g., mouth sentences responding into a microphone; foot sentences responded to with the foot). These results provide support for the theory of embodied cognition, in that they show

that language processing is grounded in bodily interaction. Specifically these findings demonstrate that the action implied by a sentence affords an action to the participant, and can either facilitate or interfere with responding.

Importantly, these experiments have not directly compared how responding to actionrelated stimuli is affected when participants have to respond with their hand or foot. That is, how does responding to action-related stimuli with the congruent effector (e.g., action-related arm stimuli being responded to with the hand, or action-related leg stimuli being responded to with the foot), or the incongruent effector (e.g., action-related arm stimuli being responded to with the foot, or action-related leg stimuli being responded to with the foot) affect responding?

Previous research by Buccino and colleagues (2005) examined how effector-specific responding (that is, responding with the arm or leg) affected responses in an auditorily presented go-no-go task. In their experiment, participants listened to action sentences that were either hand action-related, foot action-related, or abstract sentences. Half of the participants were instructed to respond with their hand when the sentence represented a concrete action, and half of the participants were instructed to respond with their foot when the sentence represented a concrete action. Participants in the hand or foot condition listened to the same action-related sentences. Buccino and colleagues found that participants were slower responding to hand compared to foot sentences with their foot. These results show that participants were slower to respond when the listened-to action sentence was congruent with the response effector. Buccino and colleagues suggest that this occurred because listening to the action sentences interferes with the motor program of the congruent effector. However, Buccino and colleagues did not compare how the same action-related sentences were responded to between effectors (e.g., hand versus foot). That is, when participants either responded with their hand or foot, but not with both.

The experiments in this chapter examined how the effector response (hand versus foot) affects responding during the semantic categorization of arm and leg stimuli. The results from Experiment 7 demonstrated a significant congruency advantage for arm stimuli, whereby participants were significantly faster and more accurate at responding to arm stimuli with their dominant hand than with their dominant foot. However, for leg stimuli a congruency advantage was not shown. The results from Experiment 8 also show a significant congruency advantage for arm stimuli, whereby participants were significantly faster at responding to arm stimuli with their dominant hand then with their dominant foot. However, for leg stimuli a congruency advantage was not shown. The results from Experiment 8 also show a significant congruency advantage for arm stimuli, whereby participants were significantly faster at responding to arm stimuli with their

non-dominant hand than with their non-dominant foot. Responding to leg stimuli produced the opposite effect, whereby participants were significantly faster and more accurate at responding to leg stimuli with their hand compared to the foot. The within-effector analyses demonstrated that the congruency advantage for hands, and the lack of a congruency advantage when responding with the feet, may be due to the hands being faster at responding to hand/arm and foot/leg stimuli compared to the feet in this task. However, the congruency advantage shown for accuracy when responding with the non-dominant hand, and the congruency advantage of 28 msec in the hand effector analysis, suggests that there may be more going on than hands being faster to respond than feet. It could be the case that with more power, a significant congruency advantage may emerge for both RT and accuracy. As such, future research should examine congruency in an experiment with additional power, but should also take into account the arm advantage shown in these experiments.

Conclusion

The results discussed in this chapter provide a novel examination of how the effector used to respond affects the processing of action-related language. Specifically, given the significant BOI advantage found in these experiments, the results support the notion that written language is grounded in sensorimotor processing. However, the results also demonstrate that there are differences in how arm and leg stimuli are processed. Furthermore, a significant congruency advantage was only shown when participants responded to hand/arm stimuli with their dominant or non-dominant congruent effector. However, the faster reaction times shown when responding with the hand may be due to the hand being faster to respond in this task. Taken together, these results not only suggest that written language is grounded in sensorimotor processing, but also indicate that arms may activate richer sensorimotor representations, resulting in arms being more grounded in bodily interaction and sensorimotor processing than legs.

CHAPTER 6

GENERAL DISCUSSION

A Summary of the Findings from Chapters 2 to 5

The aim of this dissertation was to provide a comprehensive examination of the theory of embodied cognition by comparing the processing of action-related stimuli using multiple paradigms. The results provide a novel set of findings about embodied cognition using a newly developed stimulus set and paradigm. The results from the experiments carried out in this dissertation are consistent with the theory of embodied cognition, and furthermore, provide directions to explore in future research.

The aim of Chapter 2 and 3 was to provide a neuroanatomical examination of embodied cognition. Specifically, the goal of Chapter 2 was to determine whether the sensorimotor and premotor cortices are organized somatotopically when participants provide their own actionrelated semantic representations for an object presented in word format; and furthermore, to determine whether there is evidence that the motor regions process action-related semantic information. The results from Chapter 2 demonstrate that the premotor and sensorimotor cortices respond during the processing of action-related stimuli, and furthermore, are organized somatotopically. Specifically, the results showed unique somatotopically organized activation during the arm and leg semantic generation task anterior to the motor cortex. Furthermore, the results from Chapter 2 showed shared activation for arm stimuli between the semantic generation and motor tasks which showed the same somatotopic organization in the premotor cortex. However, for leg stimuli, shared activation was only found in the occipital lobe, which was suggested to be either due to the less complex action programs associated with leg stimuli, or to the small sample size examined in Experiment 1. The goal of Chapter 3 was to replicate the results from Chapter 2 and to further examine whether the parietal lobe is also included in the network of regions activated when producing action-related semantic information. Another goal of this chapter was to determine whether the somatotopic-semantic organization found for word stimuli was also present for picture stimuli; and moreover, whether there would be shared activation between the motor localization and picture semantic generation tasks. The word semantic generation task replicated the results found in Experiment 1 showing shared activation between the motor localization and semantic generation to words in the premotor regions, and furthermore, demonstrated shared activation between the motor localization and picture semantic

generation tasks in the premotor regions. In addition, a network of unique activation for both the picture and word semantic generation tasks was shown that included the PFN. A shared network of activation was also found between the motor localization and picture and word semantic generation tasks for both arm and leg stimuli. As such, the shared activation for the motor localization and leg word semantic generation task illustrates that the lack of shared activation in the motor regions in Experiment 1 may have been due to the small sample size. The somatotopically organized shared activation for the motor localization and semantic generation tasks provide evidence consistent with the theory of embodied cognition.

The goal of Chapter 4 was to provide a behavioural analysis of the semantic generation task; specifically, examining whether there were differences in responding to arm and leg stimuli as a function of presentation format. Additionally, Chapter 4 sought to examine whether there were differences in responding to action-related stimuli in an individual post-right and an individual post-left hemispherectomy to examine the necessity of the right and left hemispheres in responding to action-related stimuli. The results from the semantic generation tasks show that participants were faster at generating a use for pictures compared to words, but did not differ on accuracy. However, for the naming task, participants were faster at naming words as compared to pictures, regardless of stimulus type (arm versus leg). In the accuracy analysis of arm stimuli, participants were more accurate when responding to pictures, whereas for leg stimuli, participants were more accurate when responding to words. Furthermore, the results show that for pictures participants were more accurate responding to arm stimuli; however, for words, there were no differences in accuracy between arm and leg stimuli. As such, these results show that pictures and words have differential access to semantic information dependent upon the type of information (action-related versus word-associated (e.g., orthography and phonology) information) and task complexity (semantic generation versus naming).

The processing of action-related stimuli in an individual post-left and an individual postright hemispherectomy was also compared to healthy control participants. The results demonstrate that both individuals showed some degree of impairment on the semantic generation and naming tasks. However, the most consistent effects were the opposing single dissociations involving the leg picture stimuli. That is, in the semantic generation task the individual with an intact right hemisphere was impaired on TDR and accuracy, whereas the individual with an intact left hemisphere performed closer to normal limits on response time and within 1 SD of the

controls' mean accuracy. In the naming task, the opposite single dissociation was found whereby the individual with an intact left hemisphere was impaired on TDR, and severely impaired on accuracy, in naming leg picture stimuli, whereas the individual with an intact right hemisphere performed closer to normal limits. These two opposing single dissociations are suggestive of a double dissociation in performance between task (naming versus semantic generation) and intact hemisphere (right versus left). These results provide evidence into the necessity of the right and left hemispheres during the processing of action-related leg stimuli, which will be discussed in more detail below.

One goal of Chapter 5 was to determine whether words that were rated as higher in BOI were responded to more quickly than words rated as lower in BOI, and furthermore, whether the relationship between RT and accuracy with BOI was affected by responding with the hand or foot. A second goal of Chapter 5 was to examine how the effector used to respond affected responding in a semantic categorization task. That is, participants were instructed to respond with either their dominant (Experiment 7) or non-dominant (Experiment 8) hand or foot when making a decision of whether a stimulus was used by the arm or leg. When responding with the dominant effector, an examination of the relationship between RT and accuracy with BOI for arm stimuli demonstrated that arm words rated as higher in BOI were responded to more quickly and accurately than arm words rated as lower in BOI, regardless of whether participants responded with their dominant hand or dominant foot. However, for leg stimuli, words rated as higher in BOI were responded to faster than words rated as lower in BOI, but only when participants responded with their dominant foot. When responding with the non-dominant effector, a BOI advantage for RT was shown for arm stimuli regardless of whether participants responded with their non-dominant hand or non-dominant foot. However, for leg stimuli, a BOI advantage was shown between RT and BOI, but only when participants responded with their non-dominant foot. Taken together, these results are consistent with the theory of embodied cognition, in that they suggest that written language is grounded in sensorimotor processing. However, these results also demonstrate that there are differences in how arm and leg stimuli are processed, in that the results suggest that arms activate a more extensive network of sensorimotor representations compared to legs. This will be discussed in further detail below.

An examination of how the effector used to respond affected the processing of hand/arm and foot/leg stimuli demonstrated differences between effectors. Specifically, when responding

with the dominant effector, participants responded significantly faster and more accurately to arm stimuli with their dominant hand than with their dominant foot. For leg stimuli, however, participants responded faster with their dominant hand than dominant foot, although this did not reach significance. When responding with the non-dominant effector, participants responded significantly faster to arm stimuli with their non-dominant hand than with their non-dominant foot. For leg stimuli, participants responded significantly faster and accurately to leg stimuli with their non-dominant hand compared to their non-dominant foot. These results suggest a congruency advantage when responding with the hand effector, and a congruency disadvantage when responding with the foot effector. However, the within-effector analyses suggest that the advantage shown when responding with the hand, and the disadvantage shown when responding with the foot, are due to hands being faster at responding in this task.

A Critical Discussion of Traditional Disembodied Theories and Embodied Theories of Semantic Memory

Proponents of the traditional models of semantic memory suggest that semantic memory is separate from perceptual and action systems (Caramazza et al., 1990; Fodor 1975; Mahon & Caramazza, 2008; Pylyshyn, 1984; Tulving, 1972; and as reviewed by Gallese & Lakoff, 2005 Barsalou, 1999; 2008b; Barsalou et al., 2003; Gallese & Lakoff, 2005). Accordingly, concepts are thought to be abstractly and arbitrarily represented in the brain, with no relation to the body and the brain regions that govern bodily movements or interactions with the environment (as reviewed by Barsalou, 1999; Gallese & Lakoff, 2005; Zwaan, 1999). Furthermore, according to Caramazza et al. (1990) the semantic system is not organized into distinctly separate systems representing modality specific information (e.g., perceptual systems, visual systems, tactile systems), but rather that semantic representations are organized as an entire abstract representation that encompasses all of this information. Thus, retrieving a conceptual representation of a chair may require perceptual understanding of how the chair is used, and although the representation of a chair contains perceptual information, this does not mean that information about that specific chair is stored in a specific perceptual system, but rather encapsulates the entire representation of a chair, which includes its perceptual features. Likewise, disembodied theories suggest that conceptual representations are abstract and symbolic and are distinct entities from sensory and motor experiences (Caramazza et al., 1990; Mahon & Caramazza, 2005; 2008). As such, traditional models of semantic memory and disembodied

models of semantic memory together suggest that conceptual representations are represented in abstract arbitrary systems with no relation between the original sensorimotor experience and the development of a conceptual representation. Hence, according to these theories, the sensorimotor system is not central to the retrieval of a conceptual representation.

Evidence reported in the literature in support of the disembodied theory of semantic processing suggests that the motor system is not required when responding to action-related language. For example, studies of apraxic patients have shown that these patients cannot manipulate an object, but are able to recognize action-words referring to the same actions (Negri et al., 2007). Furthermore, Arevalo et al. (in press) have shown that damage to the motor system following a stroke is not associated with universal deficits in the processing of action-related stimuli. Specifically, the authors found that damage to M1 was associated with deficits in responding to foot-specific stimuli more so than mouth-specific and hand-specific stimuli. Arevalo and colleagues suggest that these results are not consistent with embodied theories of semantics, because damage to the language-motor network does not entirely limit an individual's ability to respond to action-related language. They suggest that their results provide support for the idea that the motor regions, as well as other regions that process semantic information (e.g., frontal and temporal cortices), are complimentary to the processing of action-related stimuli, but not central to it. Although these patient studies suggest that the motor regions are not required when responding to action-related semantic information, there is much research countering these findings showing that the motor regions are critical when responding to action-related language. Furthermore, recent electrophysiological studies have shown that the motor regions respond to action-related information quickly after the presentation of an action word (Pulvermuller, Shtyrov, and Ilmoniemi, 2005b), which suggests that the motor system is recruited when processing action-related stimuli. I will return to this study and discuss it in more detail later in this chapter.

Alternatively, embodied cognition theorists suggest that conceptual information is grounded in perceptual and sensorimotor experiences (Barsalou, 1999; 2008a; 2008b; Barsalou et al., 2003; Barsalou, Breazeal, & Smith, 2007; Gallese & Lakoff, 2005). Additionally, Gallese and Lakoff suggest that "conceptual knowledge is embodied", whereby conceptual information is "mapped within our sensorimotor system" (pg. 456). As such, conceptual meanings are represented in the sensorimotor regions they were experienced by, and thus retrieving conceptual

meanings should activate the same sensorimotor regions (Barsalou, 1999; 2008b; Fernandino & Iacoboni, 2010; Gallese & Lakoff). Furthermore, the retrieval of the meaning of a concept requires at least the partial mental simulation of the perceptual experience associated with the concept (Barsalou, 1999; 2008b; Barsalou et al., 2003; Gallese & Lakoff, 2005; Fischer & Zwaan, 2008; Pecher, Zeelenberg, & Barsalou, 2004). For example, when an object such as a ball is experienced (that is, interacted with or perceived), the experience is stored in modalityspecific systems (e.g., visual systems representing the visual states of the ball and sensorimotor systems representing the states associated with interacting with the ball; the process by which this occurs is described by Barsalou et al., 2003). Conjunctive neurons in association areas then conjoin this information into a representation (Barsalou et al., 2003). When the conceptual representation of the ball is activated without any sensorimotor input, the conjunctive neurons reactivate the original features of the experience that were stored in memory, thus creating a partial re-enactment or simulation of how the object (e.g., ball) was used (Barsalou et al., 2003). Thus the retrieval of the conceptual representation (that is, for ball) requires the partial reenactment of these features originally encoded in memory (Barsalou et al., 2003). Hence, conceptual representations are not separable from the action and perceptual systems, but rather there is a strong relationship between conceptual representations and perceptual, or sensorimotor, processes (Barsalou, 1999; 2008b; Barsalou et al., 2003). Furthermore, according to Louwerse (2008, pg. 838), "language comprehension is based on the physical interactions and perceptual experiences comprehenders have with their environment".

There is much evidence reported in the literature and described throughout this dissertation in favour of embodied cognition. Specifically, neuroimaging research has shown that the sensorimotor and premotor cortices are activated when processing action-related stimuli (e.g., silently reading action words or listening to action-related sentences), and that this activation is organized somatotopically dependent upon the effector the stimulus represents (Boulenger & Nazir, 2010; Boulenger et al., 2009; Esopenko et al., 2008; Hauk et al., 2004; Hauk, Davis, Kherif, & Pulvermuller, 2008; Martin, 2007; Pulvermuller, 2005; Raposo et al., 2009; Tettamanti et al., 2005). In addition, behavioural research has shown that the sensorimotor properties of a sentence can affect an individual's ability to make a physical response to that sentence (Glenburg and Kaschak, 2002). Furthermore, behavioural studies have shown that the degree of physical interaction associated with a stimulus affects responding, with stimuli that are easier to interact

with being responded to faster and more accurately in tasks that target semantic, phonological, and orthographic processing (Siakaluk et al., 2008a; 2008b). Finally, studies of patients groups who have damage to the motor system and motor pathways show deficits in responding to action-related language, suggesting that the motor system is involved in responding to action-related semantic information (Bak et al., 2001; Boulenger et al., 2008; Cotelli et al., 2006a; 2006b).

Recent electrophysiological and stimulation studies have sought to provide support for the theory of embodied cognition by demonstrating that the motor system is activated during semantic processing. To determine whether the sensorimotor and premotor regions are activated during or post semantic processing, previous research has used either: 1) magnetoencephalography (MEG) to examine whether semantic processing occurs before the sensorimotor system is activated, or whether the motor system is activated quickly following the presentation of a stimulus, which would suggest that semantic processing requires the motor system; or 2) by applying TMS to the motor system to determine whether responding to action words is facilitated or inhibited when stimulation is applied to these regions. The goal of these studies was to determine whether the motor regions are activated during semantic processing, or whether motor activation occurs after semantic processing.

Using MEG, Pulvermuller et al. (2005b) examined the spatial and temporal processing of spoken face-related (e.g., eat) and leg-related (e.g., kick) action words. The authors found that face-related and leg-related words activated the frontocentral and temporal regions. Of particular interest, Pulvermuller et al found that the processing of face-related and leg-related words activated the frontocentral cortex somatotopically, whereby face-related words more strongly activated the inferior frontocentral regions, while leg-related words more strongly activated more dorsal superior central regions. Moreover, Pulvermuller and colleagues found that semantic processing occurred early in these regions, in that the inferior frontocentral and superior central regions were found to be activated approximately 170-200 milliseconds after presentation of word stimuli. The authors also found early activation peaking around 160 milliseconds in the superior temporal regions, but suggest that this activation was likely related to phonological, acoustic and lexical processing rather than semantic processing. As such, the authors suggest that access to semantic information in the frontocentral motor regions occurs quite early, suggesting that activation in these regions is not likely occurring after semantic processing takes place.

Given the findings that the motor system is involved in the processing of language, Pulvermuller et al. (2005a) sought to examine whether applying stimulation (through TMS) to the motor system affects the processing of action-related language. Sub-threshold TMS was applied to hand and leg cortical areas while participants read arm-related (e.g., grasp) and legrelated (e.g., kick) words, pseudowords, and completed a lexical decision task. The authors found that applying TMS to motor regions facilitated responses to action words. In particular, the authors found that when TMS was applied to the arm motor regions, lexical decisions to arm stimuli were faster than lexical decisions to leg stimuli, whereas when TMS was applied to the leg motor regions, lexical decisions to leg stimuli were faster than lexical decisions to arm stimuli. Based on the finding that sub-threshold TMS facilitates responding to effector-specific action-words, Pulvermuller and colleagues (2005a) proposed that the activation of the motor regions is not simply due to the motor regions being activated after semantic processing, but rather that these regions process action-related language. Furthermore, the authors suggested that the sensorimotor regions process language information that is effector-specific, and thus play a significant role in the processing of effector-specific action-words. Taken together, the findings from both studies suggest that the involvement of the motor system in the processing of actionrelated language is not simply a by-product of the semantic processing of the stimulus, but rather that the motor system plays a role in the semantic processing of the stimulus.

The functional imaging results from Experiments 1-3 are consistent with the theory of embodied cognition, in that they show that the motor system is involved in responding to actionrelated stimuli. Specifically, the results show that the sensorimotor and premotor regions are activated during the semantic generation to arm and leg picture and word stimuli. What is more is that these results also demonstrated shared, or overlapping, activation in regions that are activated during a motor localization task and during a semantic generation task where no arm and leg motor movements occurred. The shared activation between the motor and semantic tasks makes for a strong argument in support of embodied cognition, as it shows that activation of the motor system overlaps with activation for conceptual representations. These results illustrate that the retrieval of action-related semantic representations require simulation of the sensorimotor experiences that occurred when encoding information about that concept. However, research still needs to be done to determine the temporal dynamics of this system using electrophysiological methods (e.g., event-related potentials, electroencephalography and MEG) during a semantic generation task.

Interestingly, the results from Chapter 3 are consistent with previous neuroimaging research demonstrating evidence of a human MNS that responds to action-related language processing. The MNS was originally identified in the monkey premotor cortex (area F5) and inferior parietal lobe (area PF/PFG; Fernandino & Iacoboni, 2010). Mirror neurons in monkeys have been shown to respond when a monkey carries out a goal-directed action, and during the observation of goal-directed actions, goal-directed movements, and communicative gestures (Fernandino & Iacoboni; Gallese et al., 1996; Rizzolatti & Craighero, 2004). The MNS has also been shown in humans, where the human MNS responds to transitive and intransitive actions of the hands, fingers, feet, and toes (Fernandino & Iacoboni). Neuroimaging research has also shown evidence of a mirror neuron system being activated during responding to action-related language (Aziz-Zadeh et al., 2006b; Hauk et al., 2004; Tettamanti et al., 2005). The shared activation shown for the motor localization and picture and word semantic generation tasks for both arm and leg stimuli are consistent with these results. Specifically, these results demonstrate overlapping activation in the parietal, sensorimotor, and premotor cortices for both tasks. However, as discussed in Chapter 3, the identification of a mirror neuron system requires that the same regions activated during action execution be activated during action observation. As such, future research should compare activation between the semantic generation and motor localization tasks, with a task where participants observe the same actions, to determine if there are overlapping regions of activation in the PFN for all three tasks. One criticism of the mirror neuron system is that although it seems to be involved in language comprehension, it is not known whether the system is necessary or sufficient for language comprehension (Arevalo et al., in press; Fischer & Zwaan, 2008). Thus future research should examine how these three tasks (i.e., semantic generation, motor localization, and action observation) are processed in individuals with lesions to specific regions within the motor system that have been shown to have mirror properties, to examine whether damage to these regions results in deficits in responding to action-related language. Based on previous patient studies, neuroimaging research on healthy participants, and the research presented in this dissertation, it could be predicted that the mirror neuron system plays a role in the processing of action-related semantic information,

and that damage to the mirror neuron system would result in impairments in the processing of such information.

Effect of Presentation Format

The results from the fMRI experiments are consistent with previous research demonstrating that pictures and words are processed in unique (or modular) and shared (or common) regions. Furthermore, the results from Experiment 2 and 3 show that the unique activation for pictures versus words is not only found in regions that process the perceptual components of the stimulus, but also in regions that process semantic information. In addition, the analysis of shared activation between pictures and words shows a common network of activation in the PFN. This shows that regardless of the presentation format of the stimulus, the PFN is activated, suggesting that regions that process embodied stimuli are brought online regardless of the presentation format of the stimulus. The results from the behavioural experiments are consistent with previous research suggesting that pictures and words have access to different attributes or representations; and moreover, that pictures have privileged access to action-related semantic information, while words have privileged access to word-associative knowledge.

One question that arises from this research is: Why do pictures have more privileged access to action representations compared to words? The answer may lie in the idea that pictures provide an affordance of how to use an object. Gibson (1979) originally coined the term affordance to refer to the intrinsic properties of an object that provide a way of interacting with the object in the environment. Accordingly, Tucker and Ellis (2004) have suggested that even before using an object, simply attending to the object can activate the manipulation representation associated with the object. Previous research provides support for this idea, in that research has shown that an object can afford an action (Humphreys & Riddoch, 2001; Symes Tucker, & Ellis, 2007; Tucker & Ellis, 1998; 2004). Humphreys and Riddoch (2001) were interested in determining whether memory action templates were affected by the affordance of an action in a patient (M.P.) with right hemisphere neglect, who experienced deficits in finding target objects based on their perceptual properties. Humphreys and Riddoch provided M.P. with 10 everyday objects with either the objects' handle facing towards or away from M.P., and asked him to find the target object. Humphreys and Riddoch found that action memory templates were activated by the affordance of the object. For example, a cup was more likely to afford an action,

and be identified faster, if the handle was facing M.P. rather than when it was facing away from him. Furthermore, Symes and colleagues have shown that the physical structure or arrangement of an object affects how the object will be responded to. Thus, when an object is presented in picture format, the picture provides the physical structure of the object, which could hypothetically provide a use for the object. However, when an object is presented in its word format, the word does not present a visual affordance for the object, and thus does not provide an affordance of use for the object. Hence, when a word is presented and a use must be generated for the word, a greater amount of search time is required to determine the use for the object. As such, participants are faster at producing a use for an object presented in picture format because the picture affords the object's use, or in other words, affords how the object is to be manipulated (Saffran et al., 2003). Interestingly, Tucker & Ellis (2004) have shown that not only can an action affordance be provided by the object itself, or even by a picture of the object, but an action can also be afforded by presenting the object in word format. However, the results from Tucker & Ellis (2004) show that participants categorized images of objects faster than words. These results suggest that although words can also provide an affordance for an objects' use, they are categorized slower than pictures. As such, in the behavioural semantic generation tasks, participants may have been able to generate a use for pictures faster than words because the picture provided an affordance of use for the object.

Evidence in Support of the Dual Coding Theory? The results from the behavioural experiments demonstrating differential access to action-related and associative semantic information dependent upon presentation format, and the neuroimaging results demonstrating unique and shared activation for pictures and words, can also be considered consistent with Paivio's (2010) dual coding theory. The dual coding theory was developed as a response to common coding theories, whereby all semantic and syntactic features are all stored in an abstract representation (or a common coding system) within the mental lexicon (Paivio, 2010). In the common coding system there is one abstract system within the mental lexicon, and that linguistic information is stored as an abstract representation within this system (reviewed by Paivio, 2010). Common coding theories parallel traditional abstract amodal theories. However, according to Paivio (2010), the common coding system is an inadequate representation of cognitive processes, and suggests that cognition involves two functionally separate multimodal systems: a non-verbal system and a verbal system. The non-verbal system contains "perceptual properties and

affordances of objects and events", while the verbal system contains "linguistic stimuli and responses" (pg. 207). Rather than linguistic information being stored as an abstract representation, the dual coding theory suggests that the system contains mental representational units and structures. These mental representational units can be accessed differently due to different types of inputs. For example, non-verbal and verbal representations can either be activated together or separately, which means that different representations can be accessed dependent upon the presentation format of the stimulus. According to Paivio, the input for the non-verbal system consists of imagens (or pictogens) and the input for the verbal system consists of logogens. Imagens could be thought of as an equivalent to evidence collectors for pictures, and are proposed to give rise to rich conscious imagery, whereas logogens could be thought of as an equivalent to evidence collectors for words (or linguistic units). Imagens "are intrinsically meaningful" and have direct connections to meaningful semantic information, while logogens are "pointers, addresses, or clues to meaning rather than semantically meaningful themselves" (pg. 210). Paivio further suggests that verbal and non-verbal inputs differ in their accessibility to representations within the sensorimotor modality, with non-verbal inputs having access to a greater amount of sensorimotor (or perceptual) information. Thus, this suggests that common and unique forms of semantic knowledge can be accessed dependent upon the presentation format of the stimulus.

The examination of how pictures (or imagens/pictogens) and words (or logogens) are processed in this dissertation could be thought of as a behavioural and neuroanatomical examination of the dual coding theory. The neuroanatomical results show that pictures and words have access to the common semantic representations (shared processing), but also show that pictures and words have access to modular semantic representations (unique processing). This is consistent with the dual coding theory which suggests that both have access to common semantic representations, but also shows that there may be separate routes through which they are accessed. The behavioural results are also consistent with the dual coding theory. Specifically, in a task that targets action-related semantic information (semantic generation task), participants are faster at accessing action representations for pictures, whereas, in a task that does not target specific semantic information (naming tasks), participants are faster at identifying the word version of the stimuli. Again, these results suggest that both pictures and words have access to semantic information, where pictures have more direct access to action information, while

words have more direct access to a common representation system not grounded in meaning. Given that the dual coding theory suggests that imagens have direct access to meaning representations about the object's referent, then pictures being able to access action-related semantic knowledge faster than words fits with the dual coding theory. As such for the semantic generation task, when participants respond to the picture version of the object, the picture provides a direct route to how the object can be used. However, when participants respond to the word version of the task, the word does not have a direct route to the action, and thus participants have to search for the use associated with the word referent of the object. With the naming tasks, participants are faster when responding to words because they do not have to access a complex system of semantic representations to be able to name the word; rather they can quickly access this word from their internal mental lexicon. However, when participants are naming a picture, they have to search through their internal mental representations of objects to find the representation that best matches the picture. This searching for the object that best matches the target picture requires more search time than simply naming (or reading) a word.

Taken together, these results suggest that the degree of semantic processing required to complete a task, will affect how quickly an individual can perform the task. Specifically, when a task requires a great deal of semantic processing, an individual will be quicker responding to stimuli (that is, pictures) that have direct access to meaning representations compared to responding to stimuli that do not have direct access to meaning representations (that is, words). In the semantically complex task, responding to stimuli that do not have direct connections to meaning representations will increase the search time needed to find the meaning associated with the word referent of the stimulus, hence causing longer response times. In a task that requires less semantic processing to complete, the connections between the stimulus and meaning become less important. Furthermore, in the naming task, there should be even less reliance on semantic processing to identify a word compared to identifying a picture. Thus, an individual can read a word rather quickly without having to access the semantic representations of the word, whereas when naming pictures, participants may first need to access some semantic information about what the picture represents (requiring greater search time). Therefore, in the less semantically complex naming task, names of words are accessed faster than names of pictures. Given that participants show differential access to action-related semantic knowledge dependent upon the presentation format of the stimulus (pictures versus words) and due to the semantic demands of

the task (semantic generation versus naming), these results suggest that all semantic representations cannot simply be stored in an amodal semantic system separate from perceptual systems.

Processing of Action-related Stimuli Post Hemispherectomy

Previous research examining the processing of action-related stimuli in patients with damage to the motor, premotor, and motor pathways show deficits in responding to actionrelated language (e.g., Bak et al., 2001; Boulenger et al., 2008; Cotelli et al., 2006a; 2006b). These findings suggest that damage to regions within the motor system produces impairments in the processing of action-related language. According to Price et al. (2006) the only way to determine whether a brain region is necessary to perform a given task is through damage to that region. Thus, the impairment in processing of action-related stimuli in patients with damage to the motor system suggests that the motor system is necessary to perform semantic tasks involving action-related stimuli. However, to my knowledge previous research has yet to examine how action-related language is processed in an individual after the removal of an entire hemisphere, and thus the examination of the processing of action-related stimuli posthemispherectomy provided a novel examination of embodied cognition. As discussed above, both individuals showed evidence of an impairment on response times in both the semantic generation and naming tasks; however, when accuracy was examined, the only consistent impairment found was for leg picture stimuli. Specifically, during the semantic generation to leg picture stimuli, the individual with an intact right hemisphere was impaired, whereas the individual with an intact left hemisphere performed closer to normal limits. Conversely, during the naming of leg picture stimuli, the individual with an intact left hemisphere was impaired, whereas the individual with an intact right hemisphere performed closer to normal limits. As such, these results demonstrated that the right hemisphere seems to be more critical for the naming of leg pictures, while the left hemisphere seems to be more critical for the semantic generation to leg pictures.

These results provide exciting new findings into the processing of action-related stimuli post-right and post-left hemispherectomy. However, one question that remains is: Why are there differences between arm and leg stimuli in the hemispherectomy participants? That is, why do leg stimuli show the dissociation and not arm stimuli? The neuroimaging results discussed in this dissertation may provide insight in why this dissociation was found. Specifically, for arm stimuli

there was more unique activation for pictures in the frontocentral regions compared to words, whereas for leg stimuli, there was more unique activation for word stimuli in the frontocentral regions compared to pictures. The finding that for leg stimuli there was less unique picture activation in the PFN compared to words may be why leg picture stimuli showed a dissociation and leg word stimuli did not. Additionally, the neuroimaging results demonstrating that arm stimuli were processed bilaterally in the PFN, whereas leg stimuli were mainly processed in the left PFN, may provide evidence as to why leg stimuli showed a dissociation in performance but arm stimuli did not. Moreover, Arevalo et al. (in press) showed that responding to leg stimuli was more affected by lesions to the motor cortex because leg stimuli are "less salient". This suggests that if damage occurs in motor regions, leg stimuli will be more affected. However, future research should expand on this research and examine whether this dissociation is found using a larger group of hemispherectomy participants. Furthermore, it would be interesting to compare how different patient groups (e.g., Parkinson's disease and corticobasal degeneration) with damage to the premotor and motor regions would perform on these tasks given that these patient groups have difficulties responding to action-related language. Moreover, it would be interesting to compare task performance in hemispherectomy patients who have had an entire hemisphere removed with patients who have more specific, or localized, damage in order to provide increased understanding into the sufficiency and necessity of different regions during the processing of action-related stimuli.

Examining the Effect of Response Effector

The Relationship between Body-Object Interaction and the Effector used to Respond. Previous research by Siakaluk et al. (2008a; 2008b) has shown words rated as high in BOI (or those that are more embodied) are responded to more quickly and accurately than words rated as low in BOI (or those that are less embodied). According to Siakaluk and colleagues, words that are rated higher in BOI are associated with a greater amount of sensorimotor knowledge and thus activate richer action-related semantic representations, which is why participants are able to respond more quickly to high BOI words. Conversely, words rated lower in BOI are associated with less sensorimotor knowledge and thus activate fewer action-related semantic representations, which is why participants respond more slowly to low BOI words. Based on this research, one goal of Chapter 5 was to determine whether words rated as higher in BOI would be responded to more quickly with the congruent and incongruent, as well as dominant and nondominant, effectors.

The results from the current experiments show a BOI advantage for arm stimuli (that is, faster responses for high BOI arm words), regardless of effector congruence or dominance. However, a BOI advantage for leg stimuli was only shown when participants responded with the dominant and non-dominant congruent effector. As such, although both arm and leg stimuli showed a BOI advantage, this relationship is affected by the effector used to respond. These differential BOI effects shown for arm and leg stimuli could be related to differences in the network of sensorimotor representations associated with arms and legs. Specifically, it has been suggested that arms have a larger representation along the motor cortex, are associated with more extensive action-programs (Esopenko et al., 2008; Pulvermuller et al., 2005a), and activate a greater network of sensorimotor representations (based on the neuroimaging findings from Chapter 2 and 3). As such, when simultaneously activating the action-related semantic representations for arm stimuli and the motor program for hands, there should be no interference between these processes. Thus, high BOI arm words are responded to significantly faster regardless of whether they are responded to with the hand or foot. In contrast, since legs have a less extensive motor program associated with them (Esopenko et al., 2008; Pulvermuller et al., 2005a), a smaller representation along the motor cortex, and activate a narrower network of sensorimotor representations (as suggested by the neuroimaging findings from Chapter 2 and 3), the simultaneous activation of the action-related semantic representations for leg stimuli and the motor program for legs should cause interference. Thus, when participants are responding to words rated lower in BOI with their foot, interference should occur when activating the sensorimotor representations for leg stimuli and the motor program for foot simultaneously. However, when words are rated as higher in BOI they should activate more sensorimotor representations, which decreases the interference that occurs when simultaneously activating the sensorimotor representations and motor programs for the leg, resulting in faster responding. In contrast, when responding to leg stimuli with the hand there was no interference, thus how embodied a leg stimulus is does not affect responding with the hand. Taken together, these results suggest that the degree of embodiment of a stimulus (as indicated by BOI ratings) affects responding. However, the results also indicate that the differences in action programs associated with arms and legs also affect the relationship between RT and accuracy with BOI.

Congruent versus Incongruent Responding in a Semantic Categorization Task. Previous research has shown that the action implied in a sentence affects language processing when participants are required to make a physical response (e.g., ACE; Glenburg and Kaschak, 2002) Furthermore, language processing has been shown to be affected when participants have to use specific effectors to make a response. For example, Scorolli and Borghi (2007) have shown that when the effector used to make a response is congruent with the implied action in a sentence, participants respond more quickly, whereas when the effector used to make a response is incongruent with the implied action in a sentence, participants respond more slowly. Conversely, Buccino and colleagues (2005) demonstrated in an auditory language task that when the effector used to respond was congruent with the implied action of the sentence, participants were slower to respond, whereas when the effector used to respond was incongruent with the implied action of the sentence, participants were faster to respond. However, such research has not examined how having participants respond with both their hand and foot would affect responding to effector-specific action-related semantic information.

As such, one goal of Chapter 5 was to examine how responding to action-related stimuli with the congruent dominant and non-dominant effectors, or the incongruent dominant and nondominant effectors, affects responding in a semantic categorization task. When examining how responding with the dominant effector affects the categorization of arm and leg stimuli, the results showed that participants were significantly faster and more accurate at responding to arm stimuli with their dominant hand than with their dominant foot. When responding to leg stimuli, there were no significant differences in how quickly participants responded with their dominant hand compared to their dominant foot. Responding with the non-dominant effector showed a parallel pattern of results. Thus, these results suggest a congruency advantage when responding with the dominant and non-dominant hand, no congruency advantage when responding with the dominant foot, and a congruency disadvantage when responding with the non-dominant foot. However, the within-effector analyses indicated that the congruency advantage for hands, and the lack of an advantage for feet, may be due to arms being a faster effector in this type of task. The congruency advantage shown for accuracy, however, suggests that future research should be done to further examine whether a congruency advantage would be shown in both RT and accuracy in an experiment with more power to pick up effects.

Revisiting the Theory of Embodied Cognition

Based on previous fMRI experiments showing that the PFN is activated somatotopically, it can be suggested that there is spatial overlap between motor and semantic processing. Furthermore, based on previous electrophysiological research demonstrating that the motor regions are activated within 200 msec after the presentation of an action word, it can be suggested that there is a temporal relationship between motor and semantic processing. The current fMRI experiments (Experiments 1-3) demonstrating shared activation between the picture and word semantic generation tasks and motor localization tasks, and moreover the correlations in the current experiments between BOI and RT (Experiments 7 and 8) showing that words that are easier to physically interact with are responded to more quickly, suggest evidence of both a temporal and spatial relationship between motor and semantic processing. Thus, the research presented here advances the theory of embodied cognition, in that this research is consistent with both spatial and temporal overlap between motor and semantic processing. As such, when revisiting the model of embodied cognition described in the Introduction, the temporal dimension could be added to the model to account for the temporal relationship between the semantic and motor systems (Figure 17).

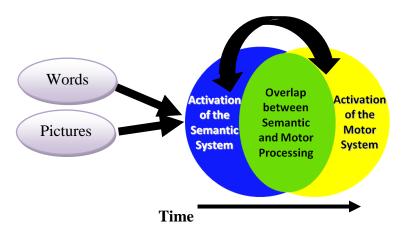


Figure 17: Revisiting the Embodied Theory of Semantic Memory. This model suggests that both semantic and motor regions are activated when responding to action-related semantic information. Furthermore, this model illustrates that there is overlap, both spatially and temporally, between conceptual and motor processing and suggests that processing action-related semantic information requires the involvement of the motor system. However, this research was not able to determine whether the semantic and motor systems are activated simultaneously, or if one system is activated prior to the other system (as represented by the dark double-ended arrow).

Directions for Future Research

One direction for future research is to develop norms on the newly created stimulus set. For example, given that pictures and words show different imagery effects when tasks target different types of linguistic or perceptual information (Paivio, 1978), it would be interesting to collect imageability ratings for pictures and words to determine: (1) whether the pictures and words used in these experiments differed on imageability ratings; and (2) whether differences in imageability can provide additional insights into the results found in the semantic generation tasks. Specifically, are the faster response times for pictures in the semantic generation tasks due to pictures having greater access to the imagery processes associated with an objects' use compared to words? Moreover, it would be interesting to examine whether the imageability of an object is related to the volume of activation produced when participants respond to actionrelated stimuli. That is, if pictures have more imagery associated with them, can this account for

why pictures seem to have more widespread activation in the semantic generation tasks compared to words?

Additionally, BOI ratings provide a good measure of the degree of embodiment of a stimulus and research has shown that higher BOI ratings of a stimulus correspond to faster and more accurate responding (Chapter 5, and Siakaluk et al., 2008a; 2008b). As such, collecting BOI ratings for both the picture and word stimuli could be one way to determine whether differences in processing are due to how easily the object is to interact with. Also, it would be interesting to examine whether the BOI ratings associated with a stimulus affect the amount (or volume) of brain activation produced when responding to that stimulus. For example, does responding to stimuli that are rated higher in BOI produce a greater (or decreased) volume of brain activation as compared to stimuli rated as lower in BOI? Finally, frequency of occurrence for the stimuli used in this experiment should be determined. For example, given that some of the stimuli consisted of multiple words, having participants rate how frequently the stimulus occurs in daily life (like the ratings developed by Tomasino, Fink, Sparing, Dafotakis, & Weiss 2008) would be one way of determining whether differences between stimuli are due to object occurrence frequency versus printed word occurrence frequency. It should be noted that using the same pictures and words in these experiments is a strong control to the extent that they both ultimately activate at least some common semantic representations. As such, the development of these norms for picture and word stimuli would provide a good way of comparing differences in both activation patterns and behavioural responses to these stimuli.

Limitations

The research discussed in this dissertation sought to provide a comprehensive examination of embodied cognition. Nonetheless, there were limitations to the research that should be acknowledged. First, most of the arm and leg word stimuli presented in this dissertation were matched using the norms from the English Lexicon Project database (i.e., word length, Kucera & Francis word frequency, Hal word frequency, and subtitle word frequency); however, some stimuli were not included in the database and thus could not be matched. In addition, the arm and leg picture and word stimuli were not matched on semantic variables such as imageability, concreteness, and number of features. Thus some of the differences in how arm and leg picture and word stimuli were responded to could be a function of the stimuli not being matched on these variables. As such, future research should match arm and leg stimuli on these

semantic variables, and additionally, should develop measures for the word stimuli that were not in the English Lexicon Project database. Secondly, arm and leg stimuli used in Chapter 5 did not have equivalent BOI ratings, in that arm stimuli ratings were both higher and less variable (i.e., 1/3 less variable) than leg stimuli ratings. This suggests that participants not only thought leg stimuli were more difficult to interact with, but also were more variable in their ratings for these stimuli. Future research should also examine whether there are differences in the processing of arm and leg stimuli when they are matched for BOI.

A third limitation in this research was that in the fMRI experiments participants completed the motor localization task before the semantic generation task, which was done so as to not have a more complex semantic task influence the processing of a basic motor task, and thus artificially increase shared regions of activation. In particular, having participants' complete arm or leg motor movements prior to the arm or leg semantic generation tasks could have primed the motor system. Thus if the motor system was primed before completing the semantic generation task, then arguably some motor activation in the semantic generation tasks could be due to priming. As such, future research should counterbalance task presentation (e.g., semantic generation task followed by the motor localization task and vice versa).

Finally, given that the hemispherectomy participants had surgery more than 30 years ago, a great deal of compensatory processing would have occurred in this time. As such, the differences in functional abilities between J.H. and S.M. shown in Chapter 4 may not be accounted for by the hemispherectomy alone, as there could be differences in how much compensation has occurred in this time. Furthermore, in those 30 years both individuals have experienced different life circumstances. Thus, some of the differences in functional abilities between these individuals may be due to variations in their life experiences following surgery (e.g., J.H. has a full time job, drives a car, is very active, and prefers face-to-face communication, while S.M. does not have a job, but participates in volunteer activities, and prefers to communicate with people on the computer or on the phone). Hence, further examination of how right and left hemispherectomy affects the processing of embodied language should be done longitudinally by examining individuals directly pre- and post-surgery with follow-up examinations at specific intervals post-surgery. This would allow for a way to examine how compensatory mechanisms and different life experiences affect recovery of function post-surgery, and specifically how it affects the processing of action-related semantic information.

Conclusion

The goal of the research carried out in this dissertation was to provide a neuroanatomical and behavioural analysis of theory of embodied cognition. FMRI and behavioural experiments were carried out to provide a comprehensive examination of embodied cognition. The functional neuroimaging results (Experiments 1-3) are consistent with the theory of embodied cognition, in that they show that the sensorimotor and premotor regions are activated when responding to action-related stimuli. Additionally, the results show that there is common activation between a motor localization and semantic generation task in the sensorimotor and premotor cortices. This supports the idea that retrieving action-related semantic information requires the simulation of motor information, and furthermore, shows that the regions that encode sensorimotor information are activated when retrieving action-related semantic information. Finally, the functional neuroimaging data demonstrates that there are both modular and common regions activated during the processing of action-related picture and word stimuli. The behavioural data (Experiments 4-6) was also consistent with previous research illustrating that pictures have privileged access to action-related semantic representations, whereas words have privileged access to word-associated information. The behavioural examination of the hemispherectomy participants showed evidence of a double dissociation between task (naming versus semantic generation) and intact hemisphere (right versus left) for leg picture stimuli. Specifically, the individual with an intact left hemisphere performed better on the semantic generation to leg picture stimuli, whereas the individual with an intact right hemisphere performed better on the naming of leg picture stimuli. In a semantic categorization task (Experiments 7 and 8), the results demonstrated a BOI advantage was shown for arm stimuli regardless of the effector used to respond, whereas for leg stimuli, a BOI advantage was only shown when participants responded with the foot effector. Moreover, the results from the semantic categorization task showed evidence of a congruency advantage when participants responded with their hand, but not with their foot. However, the within-effector results demonstrated that the congruency advantage for the hand may be due to the hand being a faster effector in the semantic categorization task. Together, these results provide a novel examination of embodied cognition, extend our understanding of differences in processing related to effector and stimulus format, and moreover, provide avenues for future research.

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Appendix A

Stimuli used in the Arm Semantic Generation and Naming Tasks









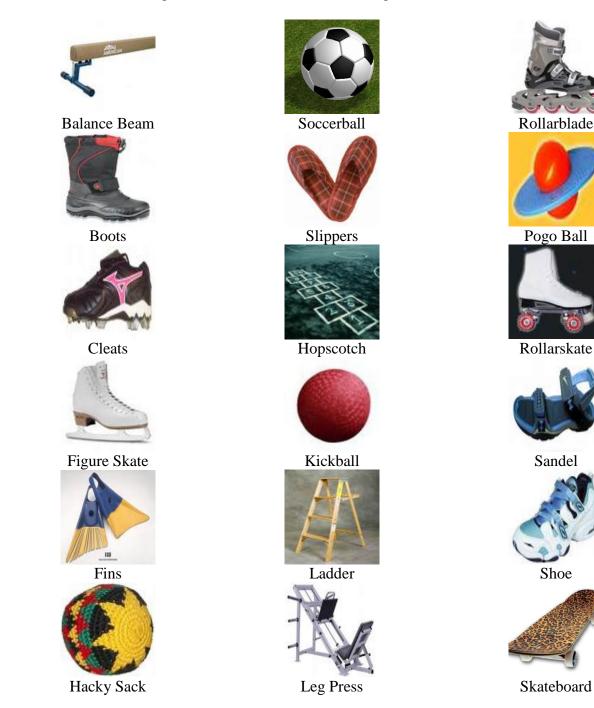
Hockey Stick







Stimuli used in the Leg Semantic Generation and Naming Tasks⁷



⁷ Five stimuli were changed in the leg semantic generation and naming tasks. The stimuli that were different between these two experiments are listed on page 147.

Sandel

Shoe





Socks



Stairs



Trampoline



Stimuli Substituted in Experiment 6 for the Naming of Leg Stimuli

In the naming tasks, Skip-it, Pogo Ball, Kickball, Rollarblade, and Rollarskate were substituted with the following stimuli:



Roller Skate



Scooter



Appendix B

Stimuli that were used in Experiment 7 and 8.

Arm Stimuli

Baseball Bat	Pen	Computer Keyboard
Baseball Glove	Piano	Pencil
Basketball	Scissors	Highlighter
Calculator	Hockey Stick	Pizza Cutter
Computer Mouse	Stapler	Potato Peeler
Doorknob	Steering Wheel	Punching Bag
Football	Spinning Top	Spatula
Rake	Beach Ball	Tennis Racquet
Frisbee	Boxing Gloves	Volleyball
Glove	Canoe Paddle	Wrench
Hand Cream	Cello	Yoyo
Key	Coffee Cup	Pool Cue
Knife	Dumbbell	Pencil Eraser
Lighter	Fork	Remote
Nail Clippers	Frying Pan	Staple Remover
Paintbrush	Acoustic Guitar	Spoon

Leg Stimuli

Balance Beam	Scooter	Moccasin
Boots	Skis	Stairmaster
Cleats	Slippers	Snowshoe
Figure Skate	Snowboard	Gas Pedal
Swim Flippers	Soccerball	Pogo Stick
Hacky Sack	Socks	Drum Pedal
Hopscotch	Stairs	Kickball
Unicycle	Dance Mat	Pogo Ball
Ladder	Diving Board	Stiletto Heel
Leg Press	Hurdle	Recumbent Bike
Bowling Shoes	Longboard	Skip-it
Rollerblade	Wakeboard	Trampoline
Roller Skate		
	Escalator	Cowboy Boot
Running Shoe	Escalator Stepper	Cowboy Boot Surfboard
		·

Appendix C

Elias, Bryden, & Bulman-Flemming (1998) Handedness and Footedness Questionnaire

Instructions: Please indicate your hand preference for the following activities by circling the appropriate response. If you **always** (i.e., 95% or more of the time) use one hand to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** (i.e., about 75% of the time) use one hand circle **Ru** or **Lu**, as appropriate. If you use both hands **equally often** (i.e., you use each hand about 50% of the time), circle **Eq**. Please do not simply circle one answer for all questions, but imagine yourself performing each activity in turn, and then mark the appropriate answer.

1. With which hand would you use a pair of tweezers?	La Lu Eq Ru Ra
2. With which hand would you use a paintbrush to paint a wall?	La Lu Eq Ru Ra
3. Which hand would you use to pick up a book?	La Lu Eq Ru Ra
4. With which hand would you use a spoon to eat soup?	La Lu Eq Ru Ra
5. With which hand would you use the eraser on the end of a pencil?	La Lu Eq Ru Ra
6. Which hand would you use to pick up a piece of paper?	La Lu Eq Ru Ra
7. Which hand would you use to draw a picture?	La Lu Eq Ru Ra
8. Which hand would you use to hammer a nail?	La Lu Eq Ru Ra
9. Which hand would you use to insert a plug into an electrical outlet?	La Lu Eq Ru Ra
10. Which hand would you use to throw a ball?	La Lu Eq Ru Ra
11. In which hand would you hold a needle while sewing?	La Lu Eq Ru Ra
12. Which hand would you use to turn on a light switch?	La Lu Eq Ru Ra
13. Which hand do you use for writing?	La Lu Eq Ru Ra
14. Which hand would you use to saw a piece of wood with a hand saw?	La Lu Eq Ru Ra
15. Which hand would you use to open a drawer?	La Lu Eq Ru Ra

16. Is there any reason (e.g., injury) why you have changed your hand preference for any of the above activities? **YES NO**

17. Have you been given special training or encouragement to use a particular hand for certain activities? **YES NO**

18. If you have answered YES to either Questions 16 or 17, please explain.

Instructions: Please indicate your foot preference for the following activities by circling the appropriate response. If you **always** (i.e., 95% or more of the time) use one foot to perform the described activity, circle **Ra** or **La** (for **right always** or **left always**). If you **usually** (i.e., about 75% of the time) use one foot circle **Ru** or **Lu**, as appropriate. If you use both feet **equally often** (i.e., you use each hand about 50% of the time), circle **Eq**. Please do not simply circle one answer for all questions, but imagine yourself performing each activity in turn, and then mark the appropriate answer.

19. Which foot would you use to kick a stationary ball at a target straight ahead?	La Lu Eq Ru Ra	
20. If you had to stand on one foot, which foot would it be?	La Lu Eq Ru Ra	
21. Which foot would you use to smooth sand at the beach?	La Lu Eq Ru Ra	
22. If you had to step up onto a chair, which foot would you place on the chair first?	La Lu Eq Ru Ra	
23. Which foot would you use to stomp on a fast-moving bug?	La Lu Eq Ru Ra	
24. If you were to balance on one foot on a railway track, which foot would you use?	La Lu Eq Ru Ra	
25. If you wanted to pick up a marble with your toes, which foot would you use?	La Lu Eq Ru Ra	
26. If you had to hop on one foot, which foot would you use?	La Lu Eq Ru Ra	
27. Which foot would you use to help push a shovel into the ground?	La Lu Eq Ru Ra	
28. During relaxed standing, most people have one leg fully extended for support		
and the other slightly bent. Which leg do you have fully extended first?	La Lu Eq Ru Ra	

29. Is there any reason (i.e. injury) why you have changed your foot preference for any of the above activities? **Yes** No

30. Have you ever been given special training or encouragement to use a particular foot for certain activities? **Yes** No

31. If you have answered YES for either question 29 or 30, please explain: