SOMATOSENSORY INVOLVEMENT IN
THE CONCEPTUAL REPRESENTATION
OF OBJECTS

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ABSTRACT

The involvement of the sensorimotor system in visual object processing is at the forefront of cognitive neuroscience research. Since the discovery of the mirror neuron system, a plethora of research has been dedicated to understanding how action influences cognition. Of particular interest to the current work is the way in which two-dimensional objects are represented in the human brain. Embodied cognition theories assert that the sensorimotor system plays a large (if not entire) role in the conceptual representation of objects. Interestingly, however, although somatosensation provides the first means of acquiring information from our environments and thus is integral to the development of conceptual representation, research has generally focused on motor system contributions to object processing. Therefore, this series of experiments will focus on unravelling the relationship between the somatosensory system and object processing. To do this, we employed two different priming paradigms, one in which vibratory stimulation served as a prime and an object picture as the target (Experiments 1 to 4), and the other where the object was the prime and the vibration the target (reverse priming task; Experiments 5 and 6). In Experiments 1 to 3, the participant was required to indicate *how* they would interact with the presented object (i.e., a semantic generation task). Results from Experiments 1 and 2 showed that object processing of graspable objects could be facilitated by a vibratory hand prime, compared to non-graspable objects (Experiment 1) and objects with foot related action affordances (Experiment 2), both of which showed no priming effects. Experiment 3 used a vibratory foot prime to investigate whether the priming effects in Experiments 1 and 2 were due semantic matching effects, such that drawing attention to a modality serves to enhance processing of objects related to that modality, and found no evidence to support this account. Experiment 4 assessed the degree to which sensorimotor representations are automatically activated using an object-naming paradigm, which showed no somatosensory priming effects, and thus no evidence for automatic somatosensory involvement. Experiment 5 utilized the reverse priming task (described above), and found evidence for faster somatosensory detection when primed with a hand object, providing converging evidence of a reciprocal relationship between the somatosensory system and object processing. Finally, Experiment 6 examined whether the results from Experiment 5 were due to matching effects (similar to Experiment 3), and found no evidence for this account. Taken together, our research provides corroborative, converging evidence that semantic knowledge about how one interacts with manipulable objects involves

sensorimotor representations in the somatosensory system. This supports theories of embodied cognition and the mirror neuron system, and extends them from the motor domain to accommodate somatosensory influences, opening a new window into exploration of how touch may be incorporated into these theories. Implications for models of the mirror neuron system, and future directions for localizing these effects using neuroimaging are discussed.

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AIP	Anterior intraparietal area
dPM	Dorsal premotor cortex
fMRI	Functional magnetic resonance imaging
hMC	Hand primary motor cortex
hSI	Hand primary somatosensory cortex
IFG	Inferior frontal gyrus
IPL	Inferior parietal lobule
IPS	Intraparietal sulcus
MC	Primary motor cortex
MEG	Magnetoencephalography
MEP	Motor evoked potential
RT	Reaction time
SI	Primary somatosensory cortex
SMG	Supramarginal gyrus
SPL	Superior parietal lobule
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation
vPM	Ventral premotor cortex

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CHAPTER 1

AN INTRODUCTION TO SENSORIMOTOR INVOLVEMENT IN CONCEPTUAL

REPRESENTATION

Experiments 1 and 2 of this chapter are based on one journal manuscript:

Ekstrand, C., Lorentz, E., Gould, L., Mickleborough, M., & Borowsky, R. (2016). More than a feeling: Semantic knowledge of graspable objects is influenced by somatosensory priming. Under revision for *Psychological Science.*

The ability to process the objects in our environment is an essential component in understanding and interacting with the physical world around us. From birth, our first means of exploring the objects in our environment is through our sense of touch, and yet touch remains one of the most underresearched senses in cognitive research. Although both the motor and somatosensory systems are engaged during object manipulation, research has generally focused on the contributions of the motor system in shaping, and eventually becoming incorporated into, semantic (i.e., conceptual) representation. However, this focus on the motor system provides an incomplete picture of the nature of how conceptual information is represented in the brain and mind, as it does not take into account how *touch* may play an integral role in object understanding. Therefore, it is imperative that the contribution of the somatosensory system to conceptual knowledge is investigated, in order to broaden our understanding of the way in which objects are processed and represented in the mind. Based on this, the present research focuses on examining the intrinsic relationship between the conceptual representation of objects and the somatosensory system, in order to gain insight into how our sense of touch is involved in our knowledge about the objects in the world around us.

The Mirror Neuron System and Conceptual Representation

The idea that the motor and sensory systems are involved in conceptual processing was previously elevated from the discovery of mirror neurons. Mirror neurons represent specific populations of neurons that activate both when an animal performs a specific object-directed action, as well as during observation of that action. They were originally discovered in the ventral premotor cortex of the macaque monkey by di Pelligrino, Fadiga, Fogassi, Gallese, Rizzolatti

(1992), and were subsequently named mirror neurons in a later publication (Gallese, Fadiga, Fogassi, and Rizzolatti, 1996). In their seminal study, di Pelligrino et al. (1992) used single cell recording of neurons in area F5 of the premotor cortex of macaque monkeys while the animal either engaged in a specific action, or observed the experimenter engaging in the same action. Their results indicated that the same neurons were activated both during motor execution as well as during action observation. The researchers interpreted the bimodal (i.e., visual and motor) nature of these neurons as an indication that they are sensitive to the *meaning* of actions. Subsequently, evidence of a similar group of neurons has been shown in the parietal cortices, including parietal area PFG (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005), as well as in the intraparietal area (Pani, Theys, Romero, & Janssen, 2014), suggesting that the mirror neuron system operates as a highly interconnected network in the primate brain.

Interestingly, mirror neurons have been shown to discharge not only upon the live execution of a motor act (i.e., when an actor is present and performing the action), but also during the observation of filmed actions. Caggiano et al. (2011) compared the magnitude of mirror neuron response in both a live setting as well as filmed setting. The monkeys observed goal-directed actions carried out by the experimenter in the live setting (in this case, watching them pick up a raisin from a stick), whereas in the filmed setting, the animals watched another monkey reach for a pepper and eat it. The results indicated that the majority of mirror neurons were activated for both live and filmed action. This is an important finding, as it allows for greater experimental control in assessing the mirror neuron system, as well as providing evidence that stimuli need not be physically present in order to elicit this neuronal response. However, it was found that a large number of neurons that responded to both filmed and live action presentation were activated more strongly by the live action than the filmed action, showing differential neuronal responses to these differing types of stimuli, which should be taken into account when examining the mirror neuron system using any type of two dimensional stimuli (including pictures).

Mirror neurons have also been shown to be activated during the observation of motor acts performed by specific tools, suggesting that information coded by mirror neurons is related to the goal of the observed motor act, regardless of how this goal is achieved. Specifically, previous research has found that mirror neuron involvement can occur when the tool of interest is known to the monkey (Ferrari, Rozzi, & Fogassi, 2005; Umiltà et al., 2008; Rochat et al., 2010; Peeters

et al., 2009; Iriki, 2006). Ferrari et al. (2005) had monkeys engage in an extended training paradigm (i.e., two months), whereby the animals observed the experimenter repeatedly perform an action with a tool. Tools in this experiment included both a stick (which was used to pick up food as well as to feed the monkey), and a pair of pliers (which were used to grasp the food in addition to feeding it to the monkey), however the monkeys did not interact with the tools directly. Single neuron recording was then performed after this exposure training. The results indicated that there was a population of neurons that responded to viewing actions carried out by the tools, but this response did not extend to tools not viewed in training. As well, they showed that neuronal responses were highest when the tool produced actions and effects that were congruent with actions in the monkey's own motor repertoire (e.g., using pliers to pick up an object is similar to picking up the object with the hands). Interestingly, however, when the monkeys were subsequently placed in an environment where use of the tool was necessary in order for them to reach a food reward, they did not engage in tool use. These results suggest that while the monkey was able to identify that the tool could achieve a certain goal, they were unable to use this information in order to perform the same action.

Canonical Neurons and Canonical Mirror Neurons

The literature reviewed thus far suggests that *actions* can be integrated into the body schema of monkeys, however it provides little insight into the nature of object representation. The affordances of objects (i.e., the sites where a goal directed action can be achieved with an object) are directly related to goal-directed actions (Gibson, 1979), and thus, should also have representations in the mirror neuron system. Evidence of another class of visuomotor neurons, known as canonical neurons, has also been found, supporting this conclusion (Murata et al., 1997; Rizzolatti & Luppino, 2001). Canonical neurons are bimodal neurons that have both motor and visual properties and are found in the lower portion of area F5. They differ from mirror neurons in that rather than firing in response to observed actions, they respond selectively to the presentation of a three-dimensional object within peripersonal (i.e., reaching) space, in addition to firing during action execution. These neurons have been shown to be relatively object specific, such that neurons that code for whole-hand grasping actions also fire in response to the observation of a large object but not a small object, whereas neurons that code for precise prehension fire during observation of a small object but not a large object. Further, they also respond to presentation of objects with similar affordances, based on the types of interactions the

object permits. This suggests that canonical neurons code for the types of actions for which a particular class of objects allow, thus supporting the conclusion that motor information is intrinsically bound to the representation of an object when it can be interacted with. Further, an additional class of neurons has been found, termed canonical-mirror neurons, which have properties of both canonical and mirror neurons. Canonical-mirror neurons have been shown to respond during action execution, object presentation in peripersonal space and, unlike canonical neurons, to observation of an action upon an object (Bonini, Maranesi, Livi, Fogassi, & Rizzolatti, 2014). As such, these neurons code not only the grasping of an object (regardless of the agent), but also the graspability of a presented object. Thus, canonical neurons and canonical mirror neurons may provide a mechanism by which object shape and function are coupled in the monkey brain, allowing for comprehension and interaction with objects in their visual world.

However, as stated previously, both canonical and canonical-mirror neurons are only active when the object is within peripersonal space, and thus activation of these neurons does not indicate that the *conceptual* representation of an object is reliant upon sensorimotor involvement. As well, while these results provide evidence that objects that are behaviourly relevant to the primate recruit the mirror neuron system, there is currently little to no evidence for mirror system involvement in representing objects that are presented in extrapersonal space. This does not, however, rule out the possibility of mirror system involvement in conceptual representation in humans, as humans have an advanced ability to understand the relationships between objects and the actions for which they afford, which is not necessarily the case for primates (Povinelli, Reaux, Theall, & Giambrone, 2000). Thus, the mirror neuron system in humans has been shown to be much more complex than in primates.

The Human Mirror Neuron System

While the mirror neuron system has been well delineated in primates, the mirror neuron system in humans has been less clear-cut. Homologues of the mirror neuron regions of monkeys have been found, suggesting the existence of an equivalent mirror system (see Figure 1). Generally well accepted is the presence of human homologue areas in the parietal cortex, including the anterior intraparietal (AIP) area, which is involved in integrating visual and motor information (Durand, Peeters, Norman, Todd, Orban, 2009), as well as the homolog for the PFG, thought to be located in the inferior parietal lobule (IPL; Orban & Caruana, 2014). Early evidence had previously implicated Brodmann area 44 in the human inferior frontal gyrus (IFG) as a

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possible homologue of area F5 in the monkey cortex (Preuss, 1995; Rizzolatti & Arbib, 1998, Rizzolatti & Craighero, 2004), and some neuroimaging studies have supported this conclusion (Cattaneo, Sandrini, & Schwarzbach, 2010; see also Avenanti, Candidi, and Urgesi, 2013 for a review). However, it has recently been suggested that task differences in these earlier studies may have led to activation in this area that is not related to the mirror neuron system and, indeed, when a recent meta-analysis was constrained to examine only studies using hand actions and passive observers, this area was not active, and instead it appears that Brodmann area 6 of the precentral gyrus is more likely to be the homologue of F5 (ventral premotor cortex; vPM; Grosbras, Beaton, & Eickhoff, 2012; see also Cerri et al., 2014). Temporal mirror neuron areas have also been identified (including the superior temporal sulcus, STS), however we will focus primarily on the parietal and frontal mirror neuron system areas. Thus, while the primate mirror neuron system is generally well understood, obtaining direct evidence for the areas involved in the human mirror neuron system using neuroimaging and physiological methods is still necessary.
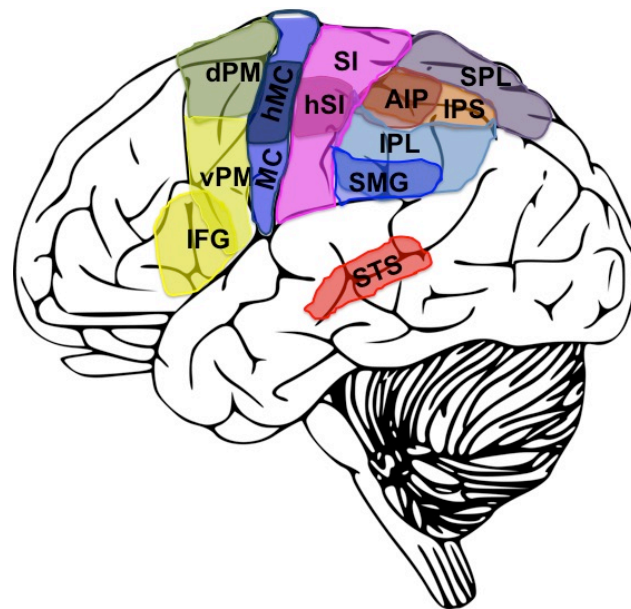
Figure 1. Key areas of the human mirror system. From anterior to posterior: IFG = inferior frontal gyrus, vPM = ventral premotor cortex, dPM = dorsal premotor cortex, MC = primary motor cortex, hMC = hand primary motor cortex, SI = primary somatosensory cortex, hSI = hand primary somatosensory cortex, AIP = anterior intraparietal sulcus, IPL = inferior parietal lobule, SPL = superior parietal lobule, SMG = supramarginal gyrus, IPS = intraparietal sulcus, STS = superior temporal sulcus. Adapted from Cattaneo and Rizzolatti (2009).

Indirect evidence for a mirror neuron system has been shown using various imaging techniques. For example, Cross, Torrisi, Losin, and Iacoboni (2013) used an imitation control paradigm during functional magnetic resonance imaging (fMRI), whereby participants viewed a video cue of a hand either lifting its index or middle finger (the imitative condition) or a video cue where a moving dot was presented on either the index or middle finger. Participants were required to make a motor response that was either congruent with the video cue (e.g., lifting the index finger when the cue index finger was lifted, or when the moving dots were presented on that finger) or incongruent. Their results indicated that there was a system of brain regions involved in identifying and resolving the imitative conflict (including the prefrontal cortex and the IFG) when the participant was required to make an incongruent action in the imitative condition. The researchers took this as evidence that the IFG and prefrontal cortex are integral components of the human mirror neuron system.

Further, evidence from Sartori, Begliomini, and Castiello (2013) used transcranial magnetic stimulation (TMS) to invoke reversible lesions in the primary motor cortex (MC). Left- and right-handed participants observed a model performing object-directed grasping actions with either their left or right hand while the experimenters monitored the participant's motor-evoked potentials (MEPs) induced by the TMS pulse. MEP amplitude acts as a measure of motor tract excitability (in this case, the corticospinal tract) associated with a specific action. Results indicated that there was a change in the MEP in the dominant hemisphere in response to the observed action regardless of whether the dominant or non-dominant effector performed the action. This suggests that motor representations are effector-independent, providing evidence of abstract encoding of movement in a higher order system that translates motor information into a format that matches the participant's hand preference. Thus, this research provides evidence of a mirror system in humans that encodes actions in terms of an individual's motor repertoire.

Of particular interest to the current studies, somatosensory activation has also been shown during the processing of action related stimuli. Tactile sensory information is processed initially in the primary somatosensory cortex (SI) before undergoing further processing in the SPL, AIP, and IPL, whereby these areas then have bidirectional projections to the dPM and vPM cortices (Hari & Forss, 1999; Petrides & Pandya, 2002). As the somatosensory cortices have been shown to have this extensive connectivity with the motor system, Avikainen, Forss, and Hari (2002) hypothesized the action observation should impact somatosensory activation. Somatosensory

evoked fields (a measure of somatosensory system involvement, which were produced in this experiment using median nerve stimulation) were recorded during a rest condition (where no task was performed), a manipulation condition (whereby the participant manipulated a small object in their hand), and an observation condition (whereby the participant observed another person manipulating the object). Results indicated that in the action observation condition, activation in SI was enhanced. Further, Woods, Hernandez, Wagner, and Beilock (2014) extended these findings beyond the visual domain, showing that when experts listened to familiar sports sounds (e.g., a basketball dribble), there was extensive activation in motor planning regions of the brain, as well as SI. Finally, somatosensory stimulation has been shown to enhance motor plasticity as a function of action observation. Bisio et al. (2015) had participants observe finger-tapping movements in conjunction with somatosensory stimulation to the median nerve of the arm. Their results indicated that there was greater corticomotor excitability in MC when visual and somatosensory information were combined, suggesting that the somatosensory system plays an important role in processing action information. Overall, these studies help to gain valuable insight into the mirror neuron system in humans, however based on the indirect nature of the tasks it is difficult to definitively identify the specific neural regions that encompass this system.

The Sensorimotor System and Three Dimensional Objects

In the absence of a complete understanding of the mirror neuron system in humans, an interesting question arises as to how objects (including tools) are represented in the human brain. As discussed earlier, while primates do engage in some tool use, it is to a much lesser extent than humans. Further, humans have an advanced ability to understand the causal relationship between tool use and the obtained results, however this is not the case for primates (Povinelli et al., 2000). Thus, the use of primate models in assessing the degree of sensorimotor and mirror system involvement in object representation in humans may not be entirely feasible, as it appears that they do not share equivalent representations among species. Indeed, even between primate species (e.g., between macaque monkeys and chimpanzees), the mirror neuron system has been shown to be quite variable and appears to have substantially evolved over time (whereby the mirror neuron system in chimpanzees is more complex than that of macaques; e.g., Hecht et al., 2013; Rozzi et al., 2006; see also Hecht & Parr, 2015 for a review). Coupled with our limited knowledge of the human mirror neuron system, exploration of the systems involved in object

representation (with an emphasis on tool use) has largely used indirect measures, which will be discussed below.

Patient research has provided compelling evidence for the integration of objects into an individual's body schema. For example, Aglioti, Smania, Manfredi, and Berlucchi (1996) reported on a patient with damage to her right hemisphere who was unable to perceive her left hand as her own. This disownership was also found to extend to objects associated with her left hand (such as a wedding ring) suggesting that the semantic representation of these objects had been incorporated into sensorimotor areas associated with that hand. In line with this, Pegna et al. (2001) reported on a patient with left spatial neglect in peripersonal space that was also apparent when engaging in tool use that extended this space. When performing a typical line bisection task (whereby individuals are asked to bisect a line in what they perceive to be the center of it, see Bowers & Heilman, 1980), the patient showed the characteristic rightward bias found in most neglect patients. Further, when asked to bisect a line beyond their reach with a tool (in this case a long stick), this rightward bias was also apparent. Interestingly, however, the patient showed no deficits in line bisection when asked to bisect the distant line using a laser pointer, suggesting that tools that extend peripersonal space may become integrated into the sensorimotor system. As such, patient data has provided further evidence that objects have the ability to become incorporated into our neural representations based on our action experience with them.

Skill Learning

Expertise has also been linked to the mirror neuron system and sensorimotor activity. Specifically, gaining expertise in motor acts through practice has been shown to result in changes in plasticity at the level of not only the brain, but also the spinal and peripheral levels. For example, Pearce, Thickbroom, Byrnes, & Mastaglia (2000) used TMS to examine possible functional reorganization of corticomotor projections of elite racquet players. Their results indicated that, in comparison to non-elite players, elite players showed enhanced corticomotor excitability in MC, in conjunction with larger asymmetries in the topographic motor map of the hand, between the dominant (playing) hand and the non-dominant hand. Further, Vogt et al. (2007) used event-related fMRI to examine changes in neural activity associated with developing motor expertise. Their results showed that novel skill learning (via observation) leads to heightened involvement of areas implicated in the mirror neuron system in comparison to observation of previously learned actions. Further, the prefrontal cortex was shown to be

selectively recruited during observation and response preparation for non-practiced actions, as opposed to the practiced actions (see also Buccino et al., 2004). Thus, the mirror neuron system appears to be engaged more strongly during motor acquisition, whereas the sensorimotor system appears to be more related to skilled actions.

Further, this effect of expertise also extends to action observation. Simple observation of a motor act in the absence of motor execution has been shown to lead to reorganization of the motor system, although to a much lesser extent than actually performing the action. In a TMS study, Stefan et al. (2005) had participants view the same action repeatedly (e.g., watching repetitive thumb movements) over a period of 30 minutes. Prior to observation, thumb movements were repeatedly elicited via a TMS pulse to MC, in order to establish a baseline direction of movement. Following the action observation training period, their results indicated that the TMS pulse elicited thumb movements that deviated in the direction of the observed thumb movements. This suggests that there was functional reorganization of the cortical regions associated with the muscles performing the action, even though the participants themselves did not actually perform the action. In addition, in a magnetoencephalography (MEG) study performed by Järvelänen, Shürman, and Hari (2004), when participants viewed the experimenter using chopsticks to transfer small objects from one plate to another, there was larger mu rhythm rebound (the recovery of a frequency band associated with sensorimotor involvement, which is indicative of the extent of motor cortex activation elicited) than if the experimenter performed a similar action without actually engaging with the object. However, mu rhythm rebound was still present during the non-goal directed action, showing that actual interaction with an object is not necessary for sensorimotor involvement. Importantly, this change in activation was positively correlated with the frequency of the participants' chopstick use, suggesting that involvement of sensorimotor areas varies as a function of personal motor experience.

Extending upon these findings, Fourkas, Bonavolontà, Avenanti, and Aglioti (2008) examined how tools may become integrated into an individual's body representation and whether or not these representations could be evoked by engaging in motor imagery (i.e., visualizing oneself performing an action). The researchers measured corticospinal excitability of the muscles in the forearm and hand of expert and non-expert tennis players while asking them to visualize themselves performing a tennis swing, a table tennis swing, or a golf drive. Results indicated that expert tennis players showed increased corticospinal activity during tennis motor imagery, but

not in the other conditions, whereas novice players showed no differences throughout the three motor imagery tasks. Thus, drawing upon semantic motor imagery also has the ability to engage sensorimotor processes, resulting in sensorimotor modulation at the peripheral level. Further, using fMRI, Grèzes, Armony, Rowe, & Passingham (2003) found evidence for canonical neurons, which responded both to object presentation as well as action execution towards the object, in the human intraparietal area and precentral sulcus, providing additional evidence that objects can be represented in the mirror neuron system.

The evidence reviewed thus far in humans has highlighted the interconnectivity of perception and action by focusing primarily on observed motor acts towards an object, but a critical question arises as to whether static object presentation evokes sensorimotor involvement. That is, are the *conceptual* representations of objects inherently bound to the sensorimotor system in humans? This has been a hotly debated topic in cognitive neuroscience over the past three decades. Almost in parallel with the discoveries related to the mirror neuron system, the extent to which there is involvement of the motor and sensory systems in conceptual representation became a prominent topic in the field of psychology. In regards to the mirror neuron system, the presence of canonical and canonical mirror neurons in monkeys (i.e., neurons that respond to mere presentation of an object) may provide a potential mechanism for a perception-action representation of objects in humans, thus rendering it plausible that the conceptual representation of at least some object-action pairs are represented in the sensorimotor system. This is supported by research by Goodale, Milner, and colleagues, who have performed extensive research on the relationship between perception and action and how it relates to the dorsal ('where/how') and ventral ('what') processing streams (see Milner & Goodale, 2006, for a review). Of particular interest, areas in the parietal lobe (most notably the IPL) have been implicated to be involved in integrating perceptual and action information, and thus as the locus of semantic action knowledge pertaining to objects. Theories that assert that the sensorimotor system plays a large part in conceptual representation are referred to as *modal* or *embodied* theories of cognition, whereas theories that assert that concepts are not inherently linked to the sensorimotor system are referred to as *amodal* or *disembodied.* This debate has led to a plethora of interesting research investigating the way that objects (such as tools) are represented in the human brain, which will be reviewed in the upcoming section.

Embodied Cognition and Conceptual Object Representation

   Amodal theories of cognition posit that conceptual representations are inherently distinct from the sensorimotor system of the brain. Therefore, concepts are seen as symbolic and abstract, requiring transformation from their sensorimotor origins (see Lachman, Lachman, & Butterfield, 1979). In contrast, modality-specific/embodied theories posit that the perceptual and motor representations that the concept arose from are intrinsically bound to the cognitive representation of that concept, both functionally and neuroanatomically (Barsalou, Simmons, Barbey, & Wilson, 2003; Kiefer & Spitzer, 2001; Warrington & McCarthy, 1987; Martin & Chao, 2001; Lakoff & Johnson, 1999). Embodied cognition theories generally converge upon two main points. First, they assert that semantic knowledge is carried by sensorimotor representations, such that the neural systems involved in forming semantic knowledge are also the systems retrieving it and thus that conceptual knowledge is based in our perceptual and motor systems (e.g., Barsalou, 2008; Gallese & Lakoff, 2005). Second, they assert that semantic representations are essentially *simulations* of the perceptual and motor information used to encode these representations, thus recruiting modality specific sensorimotor systems.

   Of particular interest to the controversy of what degree of conceptual representation resides in the sensorimotor system is the issue of how tools are represented in the human brain, which are perhaps the most well studied object stimuli in the embodied cognition literature. Tools represent an interesting class of objects as they allow for goal-directed actions to occur by extending our body space, in order to interact with and manipulate the environment. Previous research has indicated that tool use has the ability to alter conceptual representations at the neural level. In a review by Maravita and Iriki (2004), it was concluded that tools become integrated into the body schema in such a way that leads to plastic modification of the body representation in the brain, such that the tool acts as an extension of the body. Presentation of tools has been shown to activate parietal motor areas (particularly the anterior supramarginal gyrus; SMG), thus providing evidence that action properties are intrinsically bound to this type of stimuli (Chao & Martin, 2000). Further, research by Culham, Valyear, and Stiglick (2004) found that when participants silently named two-dimensional *images* of tools, there was activation in the AIP, an area implicated in the human mirror neuron system (as discussed previously). Importantly, this activation overlapped with activation found when the participant engaged in visually-guided action, suggesting that even in the absence of an overt task, tools recruit neural areas that are

critical to visually-guided grasping (see also Lewis, 2007 for a review). This research also suggested that the three-dimensional object need not be physically present to engage parietal motor areas, which is critical for theories of embodiment. The anterior SMG has also been implicated in tool processing, which is in close proximity to the AIP. Further, these two structures are thought to be highly interconnected via the dorsal IPS (Orban & Caruana, 2014), suggesting that a network of posterior parietal areas may be involved in tool processing. Thus, this research supports the conclusion that tools can become integrated into the sensorimotor system.

Behavioural evidence has also supported the idea of sensorimotor simulation in response to a presented object, therefore supporting theories of embodiment. Early research by Craighero, Fadiga, Umiltà, and Rizzolatti (1996) found evidence of a visuomotor priming effect following presentation of an object. Prior to performing a motor task (in this case, grasping a bar) participants were presented with a rectangle that was oriented at either 45 degrees clockwise or 45 degrees counterclockwise. The bar was either at the same orientation as the rectangle prime (i.e., congruent trials) or at a different orientation (i.e., incongruent trials). The participants were then required to reach out and grasp the target bar, which was occluded from their view, and a verbal cue prior to each trial indicated what orientation the target bar would occur in. The results indicated that participants were significantly faster at grasping the bar if it was at a congruent orientation to the prime. The researchers took this result to indicate that motor actions can be primed by visual stimuli, thus supporting the idea that passive viewing of an object can evoke action representations. In addition, seminal work in embodied cognition by Tucker and Ellis (1998) showed similar results when the prime was a real-world object, rather than a simple geometric shape. Participants were primed with a picture of an object with a unilateral affordance (e.g., a frying pan, whereby the object's affordance is for grasping the handle). Following this, they were asked to perform a categorization judgment of whether the object was upright or inverted using either a left or right keypress (counterbalanced between participants), thus rendering the position of the affordance irrelevant to the behavioural task. Their results indicated that participants were faster at making a motor response with the hand to which the affordance was oriented towards, suggesting that presentation of the object primed the motor system related to the relevant hand. Similarly to Craighero et al. (1996) they concluded that the object

automatically evoked sensorimotor representations that then facilitated the participant's motor response.

Further, Helbig, Graf, and Kiefer (2006) extended this finding to show that performing action is not required in order to facilitate object processing and that objects with specific affordances can facilitate processing of objects with similar affordances. Participants were primed with a picture of an object that either had a similar affordance to a target object, for example if the target was a frying pan, a dust pan prime would have a congruent action affordance for grasping, or a dissimilar action affordance, for example a banjo. Participants had significantly higher naming accuracy of the target objects when the prime had a congruent action affordance, thereby suggesting that objects automatically evoke motor representations during processing. In addition, Witt, Kemmerer, Linkenauger, and Culham (2010) found evidence for a functional role of motor simulation in the processing of manipulable objects. When participants performed a motor task (squeezing a ball) while identifying tools, it was found that the motor task interfered with processing when the object's affordance was on the same side. Finally, interference effects also vary as a function of an individual's sensory experience with an object. Yee, Chrysikou, Hoffman, and Thompson-Schill (2013) found that the more sensory experience a participant had with an object, the larger the observed motor interference effect, which highlights the integral role of the sensorimotor system in object representation. Thus, the above research supports the conclusion that action affordances of manipulable objects are intrinsically bound to their conceptual representation, therefore supporting embodied theories of object representation.

However, these results were contested in subsequent years, thus making it difficult to come to a clear conclusion about the involvement of the sensorimotor system in conceptual representation. Cant, Westwood, Valyear, and Goodale (2005) argued that Craighero et al.'s (1996) results arose primarily as a function of the prime facilitating *memory-guided* grasping, as opposed to *visually-guided* grasping, as the authors argued. As such, the prime may have served to simply facilitate the memory of a specific orientation of grasping action, rather than the grasping action itself. In their series of experiments, Cant et al. (2005) replicated the findings of Craighero et al. (1996) in the memory-guided grasping condition only. When participants were not told about the upcoming orientation of the target object (i.e., were unable to rely on previous memory of an action), no priming effects were found for grasping as a function of the visual prime. In addition, the findings of Tucker and Ellis (1998) have failed to be replicated in at least

two separate studies (Bub & Masson, 2010; Yu, Abrams, & Zacks, 2014) and further evidence from Cho & Proctor (2011) has shown that alignment effects associated with the site of the object affordance can be produced by asymmetries in the visual display rather than by motor affordances themselves. Their results indicated that the salient feature of an object biased responses with the corresponding hand, regardless of its affordance (e.g., when a teapot was presented without a handle, the location of the spout elicited similar biases to the handle as those shown in the Tucker & Ellis, 1998 study, even though the spout does not have the same action affordance). Thus, it has remained contentious as to whether the *passive* viewing of objects automatically triggers inherent sensorimotor system involvement that is functionally involved in semantic processing.

In light of this, however, and similar to the research discussed above in regards to expertise in motor imagery, compelling evidence from Kiefer, Sim, Liebich, Hauk, and Tanaka (2007) has shown that sensorimotor involvement in conceptual processing is dependent upon action experience with an object. Participants were required to categorize objects based on their motor affordances and, depending on the group, either pantomime interacting with, or point at, the object during a training period of 16 sessions lasting one hour each. Results at test indicated that objects in the pantomime group showed sensorimotor involvement during object processing, suggesting that motor information contributes to semantic processing *depending* on specific learning experience. Hence, it appears that the semantic representation of objects in the sensorimotor system is *reliant* on past individual experience. Further, Weisberg, van Turennout, and Martin (2007) trained participants to use novel objects in a goal-directed, tool-like manner, in order to examine the neural activity associated with training. Prior to motor training, participants viewed pictures of the objects during fMRI, whereby activation was limited to areas involved in object processing. Following training, an extensive network of activation was found in not only object processing areas, but also action areas (including the premotor cortex). Thus, it is possible that the lack of visuomotor priming effects in the experiments by Cant et al. (2005), Bub and Masson (2010), and Yu et al. (2014) may be in part due to participants lacking a certain amount of motor experience with the presented objects, as well as task demands that were not optimal for observing an effect.

While it remains contentious as to whether passive viewing of an object inherently necessitates sensorimotor involvement, passive viewing is not the only way to tap into the

semantic knowledge about an object. Retrieving semantic information about sensory- and motor-based properties of objects can also be used to investigate sensorimotor involvement in object representation. For example, Simmons, Ramjee, McRae, Martin, and Barsalou (2006) had participants retrieve information about an object's colour and found that, in comparison to retrieving information about the object's motion, there was heightened activity in colour perception areas of the brain (including V4). Further, in regards to word stimuli, Hauk, Johnsrude, and Pulvermuller (2004) found that when participants simply read words denoting actions associated with certain modalities (e.g., the word 'lick' is related to the tongue), there was activation in the premotor cortices associated with that modality. In addition, evidence from Schendan and Ganis (2012) has shown that engaging in motor imagery prior to presentation of an object has the ability to enhance object processing, suggesting that mental simulation mimics perception and can lead to a sustained imagistic representation that is similar to actual perceptual mechanisms. Of particular relevance to the current studies, another way of evoking semantic representation is by asking participants to retrieve information about the functional properties of objects, thus drawing upon their personal semantic knowledge of interacting with that object. Esopenko et al. (2012) had participants engage in a semantic generation task, during which they were required to indicate *how they* would interact with a presented object (in picture format) as quickly and accurately as possible during fMRI (see also Boronat et al., 2004 for a similar manipulation identification task). The stimuli in this experiment consisted of objects with primarily hand (e.g., a pen) or foot related affordances (e.g., a soccer ball). Their results indicated that there was somatotopically-organized activation in the sensorimotor and premotor cortices associated with the primary modality of interaction with the object, that were in close proximity to the activation found using motor localizer tasks for these modalities. As such, having the participant rely on their own semantic action knowledge of an object provides optimal task demands for investigating sensorimotor involvement in object representation.

It is interesting to note, however, that although touch (i.e., somatosensation) is the first sense to develop (see Gallace & Spence, 2010) and therefore provides the first means of acquiring of essential information from our environments, it has been relatively overshadowed by research focused on the motor, as well as other cognitive, systems. Thus, it remains one of the most underresearched senses in behavioural research. In light of this, a few studies have sought to investigate how somatosensory information may play a role in some types of conceptual

processing. For example, early research from Klatzky, Lederman, and Metzger (1985) contradicted the prevalent assumption at the time that the haptic system is a poor recognition device by showing that, unlike when individuals are trained to haptically identify nonsense shapes, participants showed rapid and accurate object recognition when they explored familiar, real-world objects. Further, Connell and Lynott (2010) had participants classify briefly presented words based on their sensory properties (auditory, gustatory, tactile, olfactory, visual, visuotactile; e.g., the word 'itchy' has tactile sensory properties). Their results indicated that participants showed a selective disadvantage in the conceptual processing of somatosensory stimuli, such that participants were considerably slower at classifying the tactile words into the tactile sensory category. The researchers interpreted these results as support for embodied theories of cognition, such that the conceptual system recruits the perceptual system (including the somatosensory system) for the purposes of representation, as these results are in direct concordance with the tactile disadvantage shown in perception tasks of a similar nature (Spence, Nicholls, & Driver, 2001; Turatto, Galfano, Bridgeman, & Umiltà, 2004). In addition, Ackerman, Nocera, and Bargh (2010) found evidence of somatosensory involvement in influencing social judgments and decision-making. In a series of experiments, participants were provided with an object with irrelevant tactile properties to the task (e.g., in one experiment, either a heavy or a light clipboard) and were asked to give impressions of, and make decisions about, both people and situations. Overall, their results showed that the tactile information was able to influence impressions and judgments in a systematic, metaphor-specific way (e.g., in one experiment, when the participants were holding a heavier clipboard, as opposed to a lighter one, they perceived potential job candidates as more important). Finally, James et al. (2002) found that objects previously explored haptically were responded to faster when that object was presented visually at test. As well, participants showed enhanced object processing when haptically exploring a novel object simultaneously with visual processing. Based on this, is becomes clear that the somatosensory system appears to play an essential role in conceptual processing, however its contribution in the domain of visual object processing and object representation has remained comparatively unexplored.

Therefore, this series of experiments will focus on unravelling the relationship between the somatosensory system and its involvement in object representation. Experiments 1 and 2 will examine whether the processing of manipulable objects can be enhanced using a somatosensory

prime, in comparison to non-manipulable objects (Experiment 1) and objects with foot related action affordances (Experiment 2). Following this, Experiment 3 will seek to provide evidence that this effect is not due to semantic matching, such that simply drawing attention to a specific body part serves to enhance processing of objects related to that modality, rather than a direct influence of the somatosensory system. Experiment 4 will examine the extent to which the somatosensory system is automatically involved in object processing using a naming paradigm, as it is contentious as to whether picture stimuli automatically evoke strong sensorimotor involvement. Following this, Experiment 5 will seek to provide converging evidence of a reciprocal relationship between the somatosensory system and object processing by reversing the paradigm and making the object the prime and the vibratory stimulus the target, in order to examine whether the picture prime has the ability to influence somatosensory detection. Finally, Experiment 6 will be analogous to Experiment 3, to test if the results from Experiment 5 may be due to semantic matching effects, as opposed to a direct influence of the somatosensory system.

CHAPTER 2

SOMATOSENSORY INFLUENCES ON THE PROCESSING OF MANIPULABLE OBJECTS

Experiment 1

This experiment focuses on examining the impact of somatosensory stimulation on object processing based on whether the object can be easily interacted with (i.e., graspable objects) or is difficult to interact with (i.e., non-graspable objects) using the semantic generation task developed by Esopenko et al. (2012). This task will optimize our ability to examine embodiment effects by maximizing the amount of personally-relevant sensorimotor activation elicited, thus remediating some of the limitations of previous experiments that used naming reaction times (RTs) as their dependent variable (e.g., Helbig et al., 2006). Further, by having participants draw upon their own action knowledge, we are increasing the likelihood that they will engage in motor simulation, thus maximizing the probability that the mirror system will be engaged in this task. Importantly, this paradigm allows for examination of purely somatosensory influences on object processing, without confounding somatosensory involvement with motor involvement, by using a passive somatosensory prime. Because the participant is not required to engage in any overt hand movements (as was the case in James et al.'s, 2002 study, whereby the participant actively manipulated the object to gain haptic information about it) we are able to assess the extent to which the somatosensory system is tied to semantic knowledge *independently* of the motor system, which, as of yet, has not been explored.

Hypotheses

We hypothesize that the action affordances of the graspable objects should necessitate semantic processing in the sensorimotor system (in concordance with embodied theories of object representation) and, thus, that somatosensory priming should lead to faster responses to these objects. In contrast, as the non-graspable objects do not have inherent action affordances, somatosensory priming should not lead to faster responses to these objects.

Methods

Participants. Twenty-eight university students who spoke English as their first language ($M_{age} = 21.2$, 24 right-handed) participated in this study. All participants had normal or corrected-to-normal vision. This study received ethical approval from the University of Saskatchewan Behavioral Research Ethics Board.

Stimuli. Objects consisted of coloured pictures of 30 'graspable' objects (e.g., a frying pan, a razor; see Appendix A) and 30 'non-graspable' objects (e.g., an elephant, a tractor; see Appendix B) presented randomly on a white background acquired from Google Images. A small subset of the graspable and non-graspable items were adapted from an fMRI study by Wilf, Holmes, Schwartz, and Making (2013) that were matched on visual complexity, which we used when piloting an fMRI variant of our task, resulting in four of the same objects being presented twice (i.e., two different cups, two different frying pans, two different staplers, and two different spoons).

Procedure and Apparatus. Participants were asked to identify how they would interact with a picture of a presented coloured object as quickly and accurately as possible (similar to Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; see also Boronat et al., 2004 for a similar manipulation identification task). This task was chosen in order to maximize personally relevant sensorimotor activation (e.g., Borowsky et al., 2005; Borowsky, Esopenko, Cummine, & Sarty, 2007; Esopenko et al., 2012), which would serve to optimize the potential impact of the somatosensory prime. The experiment was completed on a standard Mac computer operating as a PC with Windows OS and E-Prime 2.0 software was used to program and run the experiment (Psychology Software Tools, Inc., http://www.pstnet.com). Participants were seated approximately 100 cm from a 15-inch Compaq 7500 CRT monitor, on which the object pictures were presented. Directly in front of the participant was a 12-inch Alpine SWR-T12 Type-R subwoofer on which they placed their dominant hand, which served to provide the somatosensory prime. The subwoofer was interfaced to the E-Prime program on the computer via a Memphis PRX4.50 4-Channel amplifier.

The trial progression was as follows: participants were required to fixate on a central fixation cross until the researcher initiated each trial (see Figure 2 for a general trial progression for Experiments 1 to 4). After trial initiation, on half of the trials, a 250 ms subsonic 20 Hz tone was played through the subwoofer that served to provide the vibratory prime to the participant's dominant hand. This frequency was chosen in order to render the prime inaudible to the participant, as well as to maximize somatosensory activation at the level of the cortex by primarily activating Meissner corpuscles (sensitive to frequencies in the 2-40 Hz range), which have projections through the dorsal column/medial lemniscus pathway to the thalamus and subsequently to the primary somatosensory cortex (see McGlone & Reilly, 2010 for a review).

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On the other half of the trials there was no vibration (i.e., a 250 ms gap). Coincident with this 250 ms interval (i.e., the vibration or the gap), a 6000 Hz tone was played through a different set of speakers than the subwoofers. As the experiment was being recorded for later playback, this tone was used to indicate trial onset for use during data examination, as well as to control for possible alerting effects of the somatosensory prime in comparison to the no prime condition (as alerting signals have been shown to reliably reduce reaction time; see Callejas, Lupiàñez, Jesús Funes, & Tudela, 2005). Immediately following the prime or gap, an object picture was presented in the center of the screen. Each object appeared in both the prime and no prime conditions and the order of trials was randomly selected. Each primed and non-primed object pair was presented twice, thus resulting in 120 experimental trials.
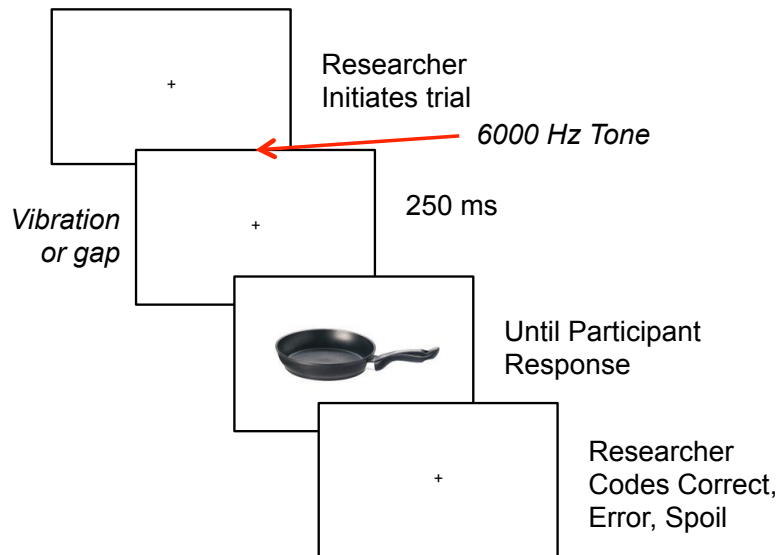
Figure 2. General trial progression for Experiments 1 to 4.

Participants were required to visualize themselves interacting with the presented object and report *how* they would interact with it, as quickly and accurately as possible, in order to optimally engage semantic systems involved in action representation. A LabTec AM-22 microphone interfaced with the E-Prime serial response box was triggered upon the participant's vocal response in order to obtain their RT for each trial. The researcher then coded '1' for a correct response, '2' for an incorrect response (i.e., if the response did not accurately describe the functionality of the presented object), and '3' for a spoil (if the microphone was triggered prematurely or failed to be triggered upon initial response). Any reasonable response to an object was accepted based on the personally relevant nature of the task. For example, if 'razor' was the

target 'shave with' or 'pick-up' would both be considered acceptable responses. There was no time limit on how long the participant had to respond and the object disappeared from the screen when the microphone voice key was triggered. Following the experimental trials, participants were required to give interaction familiarity ratings for each of the objects. The objects were randomly presented on the screen and the participant vocally indicated how familiar they personally were with interacting with the object on a scale of one to seven, whereby one was 'Very Familiar' (i.e., on a daily or near-daily basis) and seven was 'Very Unfamiliar' (i.e., never interacted with). The researcher then coded their response. Once again, there was no time limit on how long the participant had to respond.

Results

All errors and spoils were removed prior to analysis (8.5% of the total trials). We conducted a 2 (Object [Graspable, Non-graspable]) x 2 (Prime [Hand Prime, No Prime]) general linear model ANOVA on median RTs. We found a main effect of Object, $F(1, 27) = 68.00$, *MSE* $= 8163.35$, $p < .001$, $\eta_p^2 = .72$, such that graspable objects were responded to significantly faster than non-graspable objects ($M = 911.87$ and $M = 1052.70$, respectively), reflecting the expected effect of participants having greater ease describing how they would interact with the graspable objects as opposed to the non-graspable objects. The main effect for Prime was not significant, $F(1, 27) = .99$, *MSE* $= 7455.97$, $p = .33$, $\eta_p^2 = .035$, nor was the Object x Prime interaction, $F(1, 27) = 1.17$, *MSE* $= 5135.49$, $p = .29$, $\eta_p^2 = .042$ (see Figure 3 for median RTs and 95% confidence intervals using the Loftus & Masson, 1994 method. Each of the following experiments will also use these confidence intervals as error bars).
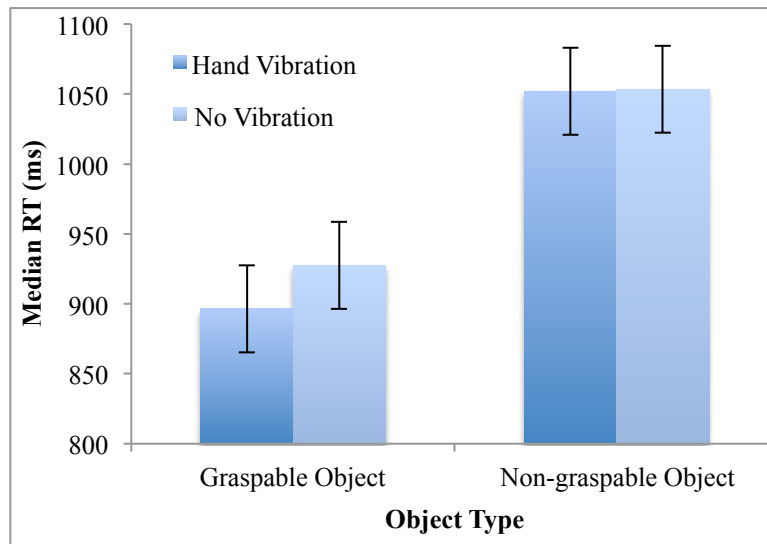
Figure 3. Median semantic generation task RT (ms) for the graspable and non-graspable objects. Graspable objects were responded to faster when preceded by the somatosensory prime. No significant RT differences were found between the Prime and No-Prime conditions for the non-graspable objects. Error bars represent 95% confidence intervals (±31.1 ms); see Loftus and Masson (1994).

Percent error rates were quite low (all less than 3.57% in each condition). There was a significant main effect of Object, $F(1, 27) = 10.45$, $MSE = 9.12$, $p = .003$, $\eta_p^2 = .28$. The main effect of Prime, $F(1, 27) = .37$, $MSE = 6.80$, $p = .55$, $\eta_p^2 = .013$, and the Object x Prime interaction were not significant, $F(1, 27) = .073$, $MSE = 12.21$, $p = .79$, $\eta_p^2 = .003$. The means and standard deviations were $M = 1.55$, $SD = 2.79$ for the Primed Graspable Object condition, $M = 3.57$, $SD = 4.70$ for the Primed Non-graspable Object condition, $M = 1.42$, $SD = 2.47$ for the No-Prime Graspable Object condition, and $M = 3.09$, $SD = 2.71$ for the No-Prime Non-graspable Object condition (see Figure 4). There was no evidence for any significant speed-accuracy trade offs.
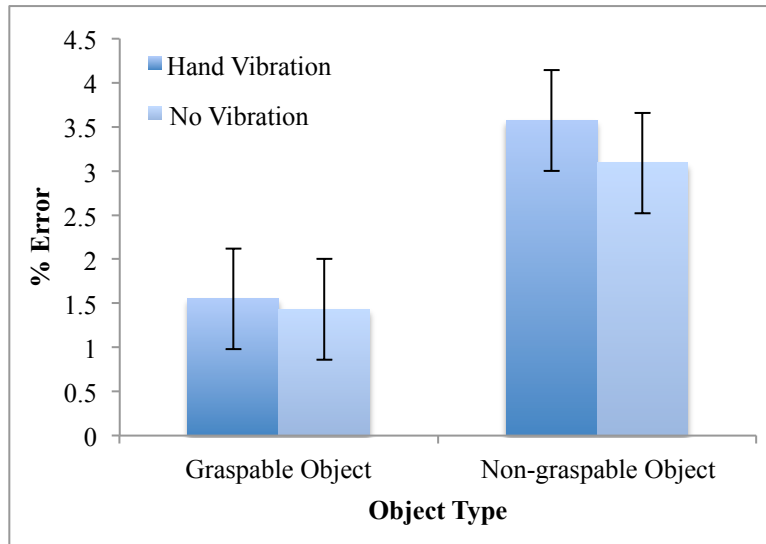
Figure 4. Percent error for the graspable and non-graspable objects. Results indicate no significant speed accuracy trade-offs. Error bars ±0.57.

Planned paired t-tests between the prime and no-prime conditions were then conducted for each object type. In support of our hypotheses on median RTs and consistent with the confidence intervals in Figure 3 (i.e., if the mean being compared is outside of the other mean's confidence interval, it supports a significant difference), results indicated that graspable objects were responded to significantly faster when preceded by the vibratory prime ($M = 896.41$, $SD = 114.58$) than when they were not primed ($M = 927.32$, $SD = 144.24$), $t(27) = -2.21$, $p = .036$, $\eta_p^2 = .15$. Non-graspable objects showed no significant differences between the prime ($M = 1051.88$, $SD = 204.72$) and no prime ($M = 1053.46$, $SD = 197.87$) conditions, $t(27) = -.060$, $p = .95$, $\eta_p^2 < .001$. When examining ratings for interaction familiarity, the non-graspable objects were found to be interacted with significantly less than the graspable objects ($M = 4.50$, $SD = .54$ and $M = 2.01$, $SD = .49$, respectively), $t(27) = -20.30$, $p < .001$, showing that participants had more motor experience with the graspable objects than the non-graspable objects.

These results were also examined using Bayesian analyses following Rouder, Speckman, Sun, Morey & Iverson (2009). This analysis allows for the researcher to examine whether the obtained results favour the null or alterative hypothesis, rather than just the alternative hypothesis (as with a standard t-test). Using the t ratios from the above t-tests, we obtained a Bayes factor of 1.29 in favour of a priming effect with the graspable items. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .56 in favour of the alternative hypothesis, providing only weak evidence of a somatosensory priming effect

(according to the strength of evidence ranges proposed by Raftery, 1995, see also Masson, 2011). The non-graspable objects resulted in a Bayes factor of 6.84 in favour of the null, and thus a posterior probability of 0.13 in favour of an effect. As well, the Bayes factor for the Object x Prime interaction (calculated using a t-test of difference scores) was 3.92, resulting in a posterior probability of .203 in favour of the alternative hypothesis.

Discussion

The results of this experiment provide preliminary evidence that graspable objects have inherent sensorimotor representations that can be influenced by a purely somatosensory prime. The somatosensory prime was shown to facilitate the processing of the graspable objects while having no impact on the non-graspable objects, which suggests that the processing of these objects relies on neural resources in the sensorimotor system, specifically, the somatosensory system, either through direct somatosensory involvement, or through its extensive interconnectivity with the motor system. However, one limitation of this experiment is the relative degree of difficulty between responding how to interact with the graspable and non-graspable objects. In the absence of a significant interaction between somatosensory stimulation and object type, it is difficult to definitively conclude that stimulation selectively improved object processing for graspable objects, but not non-graspable objects.

In support of this interpretation, the non-graspable items showed significantly longer reaction times and increased variability in comparison to the non-graspable objects, and anecdotally, participants reported greater difficulty in describing the potential interaction with these objects. It would appear that the increased reaction times in the non-graspable object condition were accompanied by too much variability in this condition to detect a potential somatosensory priming effect. Therefore, it may be tempting to argue that the somatosensory priming effect may have been due to the alerting quality of the prime rather than facilitation. Specifically, it may be possible that the vibratory prime served to facilitate responding to the graspable objects in comparison to the blank screen condition, and the lack of power in the non-graspable condition may have dampened this matching effect. However, we argue that this interpretation is unlikely based on the presence of the 6000 Hz tone prior to each trial, which should have equally alerted the participant to trial onset regardless of whether the vibratory prime was administered. Nevertheless, in the absence of a significant Object x Prime interaction, this possibility cannot be ruled out and, therefore, a more powerful experiment was sought.

Experiments 2 and 3 address the concern of increased variability in the non-graspable condition by using objects that have more easily identifiable action affordances, specifically, objects with action affordances for the feet (thus reducing the relative degree of difficulty of responding to the different types of objects).

Experiment 2

In this experiment, the graspable objects (objects associated with hand affordances; i.e., 'hand' objects) were the same as those in Experiment 1, however the non-graspable objects were replaced with items with action affordances related to the feet (i.e., 'foot' objects). These stimuli differ from the non-graspable objects from Experiment 1 in that their motor affordances are easily identifiable (e.g., 'kick' for a soccer ball). Further, if these objects *do* happen to evoke sensorimotor representations, they should be associated more strongly with the foot than with the hand (see Esopenko et al., 2012), and therefore the vibratory hand prime should not facilitate processing. This experiment will serve to help reduce the variability of responding to the two classes of objects, therefore maximizing the potential of finding interaction effects due to somatosensory priming for hand object but not foot objects.

Hypotheses

Similar to Experiment 1, we hypothesized that the hand objects will show processing benefits in the form of faster RTs when preceded by the hand vibratory prime, as these objects are thought to have inherent representations in the sensorimotor system. In contrast, the foot objects should show no processing benefits as a result of the hand prime. In addition, we expect that the two types of stimuli will be differentially influenced by the vibratory prime, resulting in a significant Object x Prime interaction.

Methods

The methods were the same as for Experiment 1, with the following exceptions.

Participants. Twenty-eight university students who spoke English as their first language (M_{age} = 20.75, 25 right-handed) participated in this study.

Stimuli. In this experiment, the non-graspable objects were replaced with 'foot' objects (e.g., a soccer ball, an ice skate; see Appendix C).

Procedure. As in Experiment 1, participants were asked to respond how they would interact with the target objects as quickly and accurately as possible. For the foot items, participants were encouraged to say actions related to the feet, rather than the hands (e.g., 'kick' for soccer ball instead of 'throw') in order to ensure that the foot objects elicited minimal sensorimotor involvement from areas associated with the hands. Trials in which the participant responded by saying hand related actions were marked as errors and removed prior to analysis.

Results

      All errors and spoils were removed prior to analysis (7.4% of the total trials). We conducted a 2 (Object [Hand Item, Foot Item]) x 2 (Prime [Hand Prime, No Prime]) general linear model ANOVA on median RTs. We found a significant main effect of Object, $F(1, 27) = 22.50$, $MSE = 5318.47$, $p < .001$, $\eta_p^2 = .46$, such that hand items were responded to significantly faster than foot items ($M = 771.49$ and $M = 836.94$, respectively). The main effect for Prime was not significant, $F(1, 27) = .91$, $MSE = 2743.31$, $p > .25$, $\eta_p^2 = .033$. Importantly, there was significant Object x Prime interaction, $F(1, 27) = 10.22$, $MSE = 1531.89$, $p = .004$, $\eta_p^2 = .28$ (see Figure 5).
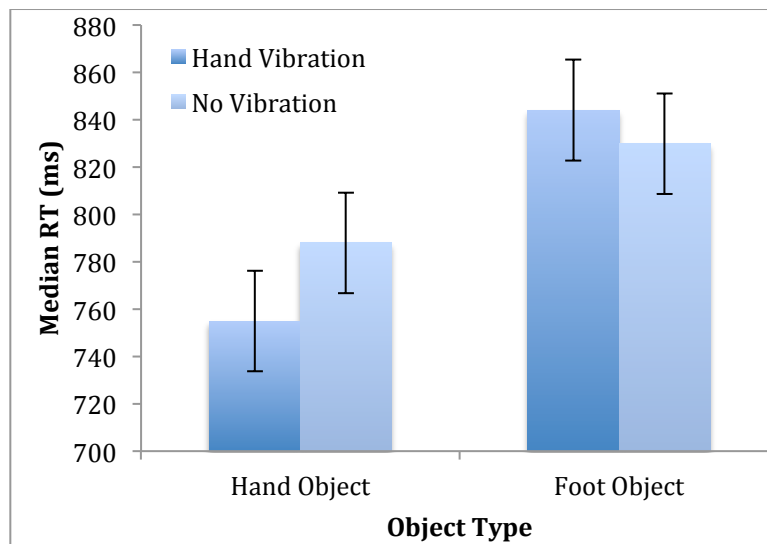
Figure 5. Median semantic generation task RT (ms) for the hand and foot objects as a function of priming. Hand objects were responded to faster when preceded by the somatosensory prime. Error bars ±21.3.

      Percent error rates were less than 3.57% in each condition. We found a significant main effect of Object, $F(1, 27) = 6.08$, $MSE = 9.41$, $p = .020$, $\eta_p^2 = .18$. The main effect for Prime was not significant, $F(1, 27) = .94$, $MSE = 6.76$, $p = .34$, $\eta_p^2 = .034$, nor was there a significant Object x Prime interaction, $F(1, 27) = .30$, $MSE = 5.29$, $p = .59$, $\eta_p^2 = .011$. The means and standard deviations were $M = 1.90$, $SD = 2.79$ for the Primed Hand Object condition, $M = 3.57$, $SD = 4.70$ for the Primed Foot Object condition, $M = 1.67$, $SD = 2.31$ for the No-Prime Hand Object condition, and $M = 2.86$, $SD = 3.23$ for the No-Prime Foot Object condition (see Figure 6). There was no evidence of any significant speed-accuracy trade-offs.
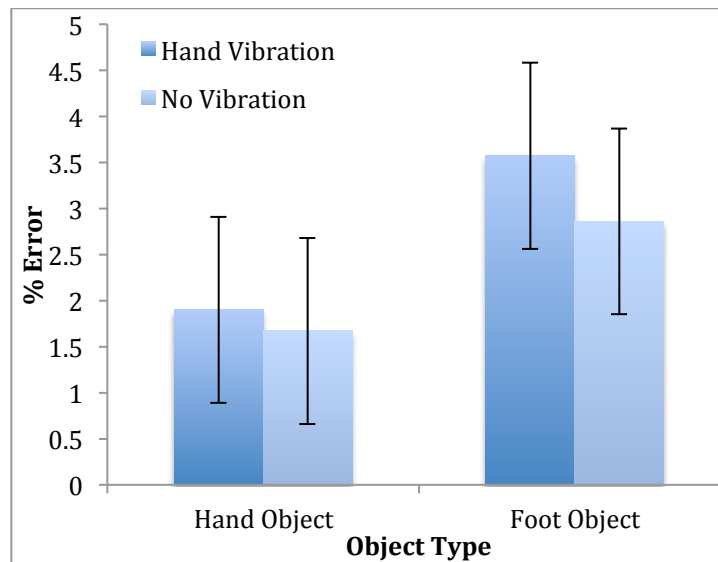
Figure 6. Percent error for the hand and foot objects as a function of priming. There is no evidence of any significant speed/accuracy trade-offs. Error bars ±1.01.

Planned paired t-tests on median RTs between the prime and no-prime conditions were conducted for each object type. Results indicated that hand items were responded to significantly faster when preceded by the vibratory prime ($M = 754.95$, $SD = 102.25$) than when they were not primed ($M = 788.04$, $SD = 106.19$), $t(27) = -3.62$, $p = .001$, $\eta_p^2 = .33$. Foot items showed no significant differences between the prime ($M = 844.04$, $SD = 136.52$) and no prime ($M = 829.84$, $SD = 122.44$) conditions, $t(27) = .95$, $p > .25$, $\eta_p^2 = .033$.

Bayesian analysis examining priming effects in the hand items showed a Bayes factor of 26.13 in favour of an effect. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .963 in favour of the alternative hypothesis, providing strong evidence of an effect. The priming effects for the foot objects resulted in a Bayes factor of 4.44 in favour of the null, and thus a posterior probability of 0.184 in favour of an effect. As well, the Bayes factor for the Object x Prime interaction was 9.82, resulting in a strong posterior probability of .908 in favour of the alternative hypothesis.

Once again, when examining ratings for interaction familiarity, the foot objects were found to be interacted with significantly less than the hand objects ($M = 5.02$, $SD = .56$ and $M = 2.37$, $SD = .43$, respectively), $t(27) = -32.59$, $p < .001$, showing a similar pattern to the non-graspable objects from Experiment 1. In comparing the non-graspable objects from Experiment 1

with the foot items in this experiment we found that, as expected, the response times to the foot items were significantly faster than the response times to the non-graspable items, $F(1, 54) = 25.62$, $MSE = 50870.04$, $p < .001$, $\eta_p^2 = .32$. Further, Levene's test showed significantly different variances between the non-graspable and foot objects, such that the foot objects had less variance than the non-graspable objects, $F(1, 54) = 6.44$, $p = .014$ in the Prime condition, and $F(1, 54) = 4.99$, $p = .030$ in the No Prime condition.

Discussion

Similar to Experiment 1, results from Experiment 2 show that pre-activating the somatosensory system has the ability to aid processing of objects with hand affordances. As the hand objects were shown to be processed faster when preceded by the somatosensory prime while foot objects showed no processing benefits, our results provide strong support that the conceptual representation of how one interacts with these hand objects is held, at least in part, in the somatosensory system. Further, as both the hand and foot objects had easily identifiable action affordances, but differed based on the site of action affordance, we were able to examine the contribution of the somatosensory system to the objects with hand affordances only. Importantly, the presence of an interaction between priming and object type illustrates differential effects between these two types of stimuli as a function of somatosensory stimulation. This indicates that vibratory priming of the hand does not simply serve to better alert one to the upcoming target (as discussed as a possible interpretation of the results of Experiment 1) and, instead, that it aids retrieval of semantic knowledge about how one interacts with objects. As well, based on the significantly different interactability ratings between the hand and the foot objects, this experiment also supports research that has found effects of expertise in sensorimotor involvement in object processing (e.g., Kiefer et al., 2007; Weisberg et al., 2007). As the hand objects were found to be interacted with significantly more than the foot objects *and* were shown to influenced by the somatosensory prime, this provides evidence that the extent to which an individual is familiar with interacting with an object influences the extent of its representations in the somatosensory system.

A potential limitation of this study is, however, that it is possible that drawing attention to the hand (via the vibration) served to simply evoke the semantic concept of a hand, thus speeding responses to objects associated with the hand that was not directly related to activation of the somatosensory cortex. Thus, it is possible that the results of this experiment are due to simple

matching between the target and the prime, such that a drawing attention the hand (via the hand vibration) creates expectations that a hand object will occur. In order to address this question, Experiment 3 will examine whether there are similar matching processes found for the foot objects, such that drawing attention to the foot (via a foot vibratory prime) serves to enhance processing of the foot objects.

Experiment 3

This experiment seeks to examine the impact of a foot vibratory prime on object processing, in order to assess whether vibration from a modality other than the hand has the ability to influence object processing. As well, it seeks to examine whether the priming effects found in Experiments 1 and 2 may be due to matching processes, such that the vibratory prime creates an expectation of which target will appear (i.e., a hand object following a hand prime). To test this, the hand vibratory prime will be replaced with a foot vibratory prime, which will allow us to examine whether foot objects show a matching effect with the foot prime.

Hypotheses

In this experiment, it is hypothesized that there will be no influence of the foot somatosensory prime on object processing and no evidence of matching effects. Specifically, the foot objects should not show systematically faster reaction times as a function of the foot prime, as these objects should not evoke strong somatosensory representations based on their primarily foot affordances. Further, as evidenced in Experiment 2, the foot objects lack the same degree of interactive experience as the hand objects, thus further supporting the idea that they should have minimal somatosensory representations. As such, for both the foot and hand objects, it is not expected that there will be any influence of the foot prime.

Methods

The methods and participants were the same as for Experiment 2, with the following exceptions.

Procedure. In this experiment, the hand vibratory prime was replaced with a foot vibratory prime.

Results

All errors and spoils were removed prior to analysis (7.8% of the total trials). We conducted a 2 (Object [Hand Item, Foot Item]) x 2 (Prime [Foot Prime, No Prime]) general linear model ANOVA on median RTs. We found a main effect of Object, $F(1, 27) = 18.25$, $MSE = 10460.52$, $p < .001$, $\eta_p^2 = .40$, such that hand items were responded to significantly faster than foot items ($M = 781.58$ and $M = 864.16$, respectively). The main effect for Prime was not significant, $F(1, 27) = .19$, $MSE = 2178.34$, $p > .25$, $\eta_p^2 = .063$. The Object x Prime interaction was also not significant, $F(1, 27) = .46$, $MSE = 5134.00$, $p = .50$, $\eta_p^2 = .017$ (see Figure 7).
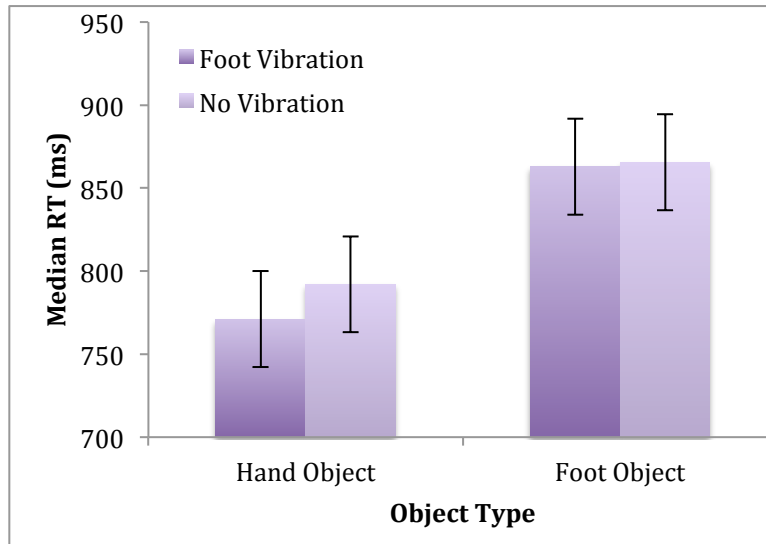
Figure 7. Median semantic generation RT (ms) for the hand and foot objects as a function of foot priming. No significant RT differences were found between the Prime and No-Prime conditions for either the hand or foot objects. Error bars ±28.9 ms.

Percent error rates were less than 3.57% in each condition. There was a significant main effect of Object, $F(1, 27) = 11.79$, $MSE = 6.07$, $p = .002$, $\eta_p^2 = .30$. The main effect for Prime was not significant, $F(1, 27) = .10$, $MSE = 7.66$, $p = .75$, $\eta_p^2 = .004$, nor was there a significant Object x Prime interaction, $F(1, 27) = .057$, $MSE = 5.17$, $p = .81$, $\eta_p^2 = .002$. The means and standard deviations were $M = 1.87$, $SD = 2.78$ for the Primed Hand Object condition, $M = 3.57$, $SD = 3.25$ for the Primed Foot Object condition, $M = 1.80$, $SD = 2.84$ for the No-Prime Hand Object condition, and $M = 3.30$, $SD = 3.70$ for the No-Prime Foot Object condition (see Figure 8). There was no evidence of any significant speed-accuracy trade-offs.
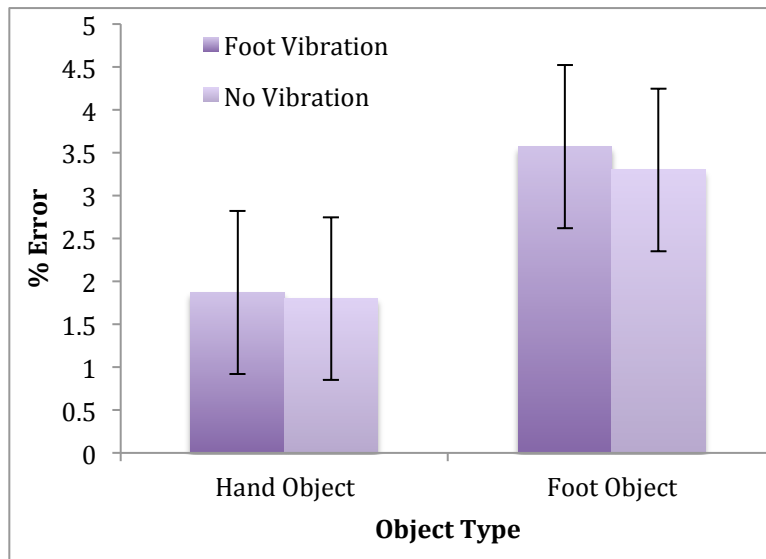
Figure 8. Percent error for the hand and foot objects as a function of foot priming. There is no evidence of any significant speed/accuracy trade-offs. Error bars ±0.95.

Planned paired t-tests on median RTs between the prime and no-prime conditions were conducted for each object type. Results indicated no significant differences for the hand objects in the prime condition ($M = 771.02$, $SD = 106.47$) versus the no-prime condition ($M = 792.14$, $SD = 142.96$), $t(27) = -1.61$, $p = .12$, $\eta_p^2 = .087$. Foot items also showed no significant differences between the prime ($M = 862.82$, $SD = 182.24$) and no prime ($M = 865.50$, $SD = 137.44$) conditions, $t(27) = -.14$, $p = .89$, $\eta_p^2 = .001$.

Bayesian analysis examining priming effects in the hand items showed a Bayes factor of 2.06 in favour of the null. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .327 in favour of the alternative hypothesis. The priming effects for the foot objects resulted in a Bayes factor of 6.79 in favour of the null, and thus a posterior probability of 0.128 in favour of an effect. As well, the Bayes factor for the Object x Prime interaction was 5.48 in favour of the null, resulting in a posterior probability of .15 in favour of the alternative hypothesis.

The ratings for interaction familiarity are shown in Experiment 2, as participants performed both the hand vibration and foot vibration conditions in the same session.

Comparison of Experiments 2 and 3

Because the hand vibration and foot vibration experiments were performed within subjects, we also conducted comparisons between them. This allowed us to examine whether

participants were responding similarly to the objects in both of the experiments (i.e., differential results are not confounded by inherent differences in RT).

Impact of experiment on object processing. To examine whether or not responses to the objects were similar between Experiment 2 (hand vibration) and Experiment 3 (foot vibration), we conducted a 2 (Experiment [Experiment 2, Experiment 3]) x 2 (Prime [Prime, No Prime]) x 2 (Object [Hand Object, Foot Object]) general linear model ANOVA. Results showed a significant main effect of Object, $F(1, 27) = 24.70$, $MSE = 9272.68$, $p < .001$, $\eta_p^2 = .48$, such that hand items were responded to significantly faster than foot items ($M = 762.99$ and $M = 853.43$, respectively). The main effect for Prime was significant, $F(1, 27) = 33.62$, $MSE = 3620.37$, $p < .001$, $\eta_p^2 = .56$. The main effect for Experiment was not significant, $F(1, 27) = 3.48$, $MSE = 48048.74$, $p = .073$, $\eta_p^2 = .11$. There was a significant Experiment x Prime interaction, $F(1, 27) = 40.88$, $MSE = 1892.78$, $p < .001$, $\eta_p^2 = .60$. The Experiment x Object interaction was not significant, $F(1, 27) = 1.19$, $MSE = 5416.19$, $p = .28$, $\eta_p^2 = .042$, nor was the Object x Prime interaction, $F(1, 27) = .3.21$, $MSE = 3540.84$, $p = .084$, $\eta_p^2 = .11$. The Experiment x Prime x Object interaction was also not significant, $F(1, 27) = 1.71$, $MSE = 2893.90$, $p = .20$, $\eta_p^2 = .059$.

Of particular interest, to investigate whether the type of prime differentially impacted processing of the objects, we performed a 2(Experiment [Experiment 2, Experiment 3]) x 2(Object [Hand Object, Foot Object]) on the primed conditions only. Results showed a significant main effect of Object, $F(1, 27) = 24.70$, $MSE = 9272.68$, $p < .001$, $\eta_p^2 = .48$, such that hand items were responded to significantly faster than foot items ($M = 762.99$ and $M = 853.43$, respectively). The main effect for Experiment was not significant, $F(1, 27) = .33$, $MSE = 26081.19$, $p = .57$, $\eta_p^2 = .012$. The Object x Prime interaction was also not significant, $F(1, 27) = .011$, $MSE = 4799.86$, $p = .92$, $\eta_p^2 = .000$, suggesting that regardless of the vibration location, both the hand and foot objects were responded to similarly in both experiments and thus that the nature of the prime is not responsible for the differential results found between these experiments.

Discussion

Results from Experiment 3 provide evidence that the results from Experiment 2 did not arise as a function of matching effects between the prime and the object type. As participants did not show facilitated responses to the foot items when primed with a vibration to the foot, there is no evidence that simply drawing attention to the relevant modality serves to aid in object processing. This is an important finding, as it suggests that the somatosensory stimulation itself,

and not other stimulus properties, is driving the facilitative effect for the hand objects. Further, this experiment supports the idea that somatosensory involvement is modality-specific, as somatosensory stimulation to the foot did not significantly influence responses to the hand objects, and thus the sensorimotor representation of the hand objects appears to be isolated to the hand modality. However, based on the obtained p-value of .12, there is a trend towards the foot vibration increasing response times to the hand objects, which may reflect some degree of interconnectivity between foot somatosensation and hand object processing. Thus, future research is necessary to uncover in which instances somatosensory stimulation can enhance object processing in order to more fully address whether somatosensory influences are modality specific (e.g., somatosensory stimulation to the arm or torso, which are in close proximity somatotopically to the hand region of SI). Regardless, these results do not provide support that the somatosensory priming effects for the hand objects in Experiments 1 and 2 are a result of matching processes between the prime and the object type.

CHAPTER 3

DEPTH OF PROCESSING AND THE AUTOMATICITY OF SOMATOSENSORY

REPRESENTATIONS

Experiment 4

In the experiments reported thus far, participants have been required to rely on the action characteristics of objects to tap into their semantic representations. However, based on the controversy in the field as to whether shallow processing of objects inherently leads to sensorimotor involvement, it is important to also examine how the somatosensory prime may influence simple object naming. While research by Tucker and Ellis (1998) and Helbig et al. (2006; as discussed in the introduction) provided support for *automatic* sensorimotor simulation when processing pictures of objects, evidence from Bub and Masson (2010), Yu et al. (2014), and Cho and Proctor (2011) has contested these results. Therefore, this experiment will utilize a naming paradigm in order to examine whether the results found when requiring the participant to attend to the action related semantic representation of the object would be similar to those found when they are not required to retrieve this information. By making the action information irrelevant to the task, it would be expected that the sensorimotor activation evoked from viewing the two-dimensional object stimuli would be greatly diminished or, potentially, entirely absent, thus dampening the influence of the somatosensory prime.

Hypotheses

In line with the findings of Bub and Masson (2010), Yu et al. (2014), and Cho and Proctor (2011), it is hypothesized that there will be no effect of somatosensory stimulation on naming for either of the object types. Thus, in contrast to Experiment 2, the somatosensory prime should not facilitate processing of the hand objects.

Methods

The methods were the same as for Experiment 2, with the following exceptions.

Participants. Twenty-eight university students who spoke English as their first language (M_{age} = 19.14, 26 right-handed) participated in this study.

Procedure. Instead of responding how they would interact with the object (Experiments 1, 2, and 3), participants were asked to simply name the object presented on the screen as quickly and accurately as possible.

Results

In concordance with the results reported above, we conducted a 2 (Object [Hand Item, Foot Item]) x 2 (Prime [Hand Prime, No Prime]) general linear model ANOVA on median RTs, and all errors and spoils were removed prior to analysis (9.6% of the total trials). We found a main effect of Object, $F(1, 27) = 53.84$, $MSE = 3442.06$, $p < .001$, $\eta_p^2 = .67$, such that hand items were responded to significantly faster than foot items ($M = 605.70$ and $M = 687.05$, respectively). The main effect for Prime was not significant, $F(1, 27) = 2.19$, $MSE = 956.95$, $p = .15$, $\eta_p^2 = .075$. The Object x Prime interaction was also not significant, $F(1, 27) = .001$, $MSE = 1367.54$, $p = .97$, $\eta_p^2 = .000$ (see Figure 9).
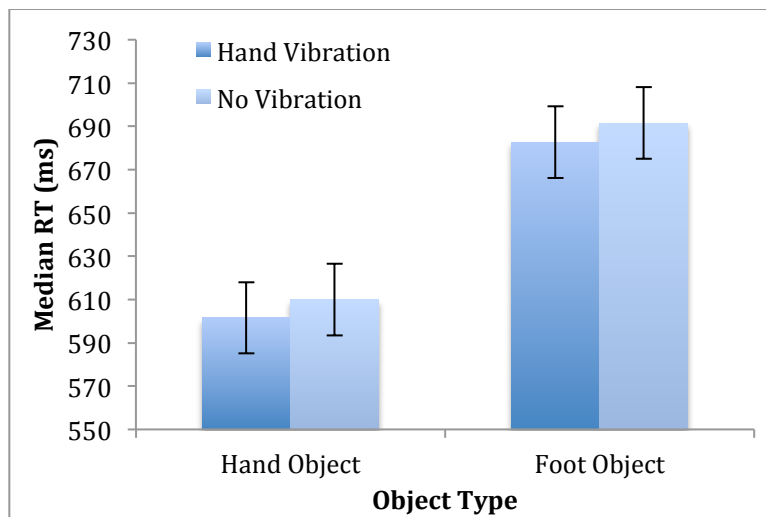
Figure 9. Median naming RT (ms) for the hand and foot objects. No significant RT differences were found between the Prime and No-Prime conditions for either the hand or foot objects. Error bars ±16.5 ms.

Percent error rates were less than 5.83% in each condition. There was a significant main effect of Object, $F(1, 27) = 34.02$, $MSE = 19.92$, $p < .001$, $\eta_p^2 = .56$. The main effect for Prime was not significant, $F(1, 27) = .15$, $MSE = 12.07$, $p = .70$, $\eta_p^2 = .006$, nor was there a significant Object x Prime interaction, $F(1, 27) = .003$, $MSE = 12.14$, $p = .96$, $\eta_p^2 = .000$. The means and standard deviations were $M = .88$, $SD = 1.81$ for the Primed Hand Object condition, $M = 5.83$, $SD = 6.38$ for the Primed Foot Object condition, $M = .65$, $SD = 1.42$ for the No-Prime Hand Object condition, and $M = 5.54$, $SD = 5.08$ for the No-Prime Foot Object condition (see Figure 10). There was no evidence of any significant speed-accuracy trade-offs.
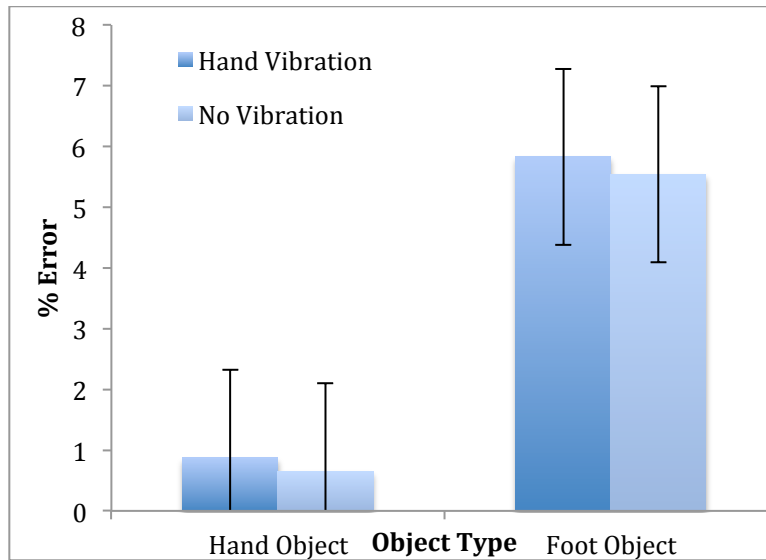
Figure 10. Percent error for the hand and foot objects as a function of hand priming. There is no evidence of any significant speed/accuracy trade-offs. Error bars ±1.45.

Planned paired t-tests on median RTs between the prime and no-prime conditions were conducted for each object type. Results indicated no significant differences for the hand objects in the prime condition ($M = 601.50$, $SD = 50.72$) versus the no-prime condition ($M = 609.89$, $SD = 61.93$), $t(27) = -1.17$, $p = .25$, $\eta_p^2 = .048$. Foot items also showed no significant differences between the prime ($M = 682.61$, $SD = 94.00$) and no prime ($M = 691.50$, $SD = 90.14$) conditions, $t(27) = -.83$, $p = .41$, $\eta_p^2 = .025$.

Bayesian analysis examining priming effects in the hand items showed a Bayes factor of 3.58 in favour of the null. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .22 in favour of the alternative hypothesis. The priming effects for the foot objects resulted in a Bayes factor of 4.92 in favour of the null, and thus a posterior probability of 0.17 in favour of an effect. As well, the Bayes factor for the Object x Prime interaction was 6.85 in favour of the null, resulting in a posterior probability of .13 in favour of the alternative hypothesis.

Similarly to Experiments 2 and 3, when examining ratings for interaction familiarity, the foot objects were found to be interacted with significantly less than the hand objects ($M = 5.20$, $SD = .51$ and $M = 2.49$, $SD = .40$, respectively), $t(26) = -32.93$, $p < .001$. The data of one participant's ratings was lost due to a program malfunction.

Discussion

Results from this experiment suggest that simple viewing and naming of two-dimensional objects is not sufficient to evoke strong sensorimotor involvement, and thus no somatosensory priming effects. This may be due to two possible explanations. First, two-dimensional stimuli may not automatically recruit the sensorimotor system and, thus when action features of the object are not necessary for the task this system is not involved. Conversely, it may be possible that this type of stimulus *does* still necessitate sensorimotor involvement, however it is to a much lesser degree than during the semantic generation task.

The results from this experiment provide interesting implications for the effect of context on the degree to which there is involvement of the sensorimotor system. Further, these results suggest that it is possible that inconsistencies in task demands of previous researchers experiments may contribute to differential results and, therefore, that researchers should employ a variety of tasks that elicit differing levels of processing to tap into the semantic representation of objects when attempting to investigate sensorimotor involvement. However, it is also possible that the variability in this task (i.e., responses to foot objects were still significantly slower than responses to hand objects), though greatly reduced from the above experiments, may still serve to diminish the power available to see an effect of the somatosensory prime. Therefore, Experiment 5 will attempt to remediate this by rendering the object stimuli irrelevant to the task, thus eliminating this variability. As well, flipping the task will allow us to examine whether significant somatosensory priming effects can be found in the reverse direction, such that hand objects prime sensory detection of hand stimulation. This would be an important demonstration for illustrating that these objects have somatosensory representations, as it follows logically that if they do elicit somatosensory system activation, this should be able to influence somatosensory detection.

CHAPTER 4

THE IMPACT OF OBJECT PRIMES ON SOMATOSENSORY DETECTION

Experiment 5

This experiment seeks to provide converging evidence for a relationship between somatosensory involvement and the processing of hand objects by flipping the task in the earlier experiments. Participants were required to detect whether the hand vibration was present or absent after being primed by either a hand or foot object. This also serves to eliminate the apparent differences between responding to the hand and foot items in order to see if the objects have the ability to prime the somatosensory system and therefore aid in detection of the vibratory stimulus.

Hypotheses

We hypothesized that hand object primes will lead to faster 'yes' responses in the presence of a hand vibration than 'no' responses in the absence of a vibration, whereas foot object primes should not speed detection of a vibration. Further, we hypothesize that RTs will be fastest in the hand object prime/vibration present condition in comparison to all other conditions, particularly the foot object prime/vibration condition, as this would indicate that hand objects are affecting somatosensory detection.

Methods

The methods for Experiment 5 were similar to Experiment 2, with the following exceptions.

Participants. Twenty-eight university students who spoke English as their first language (M_{age} = 20.71, 25 right-handed) participated in this study.

Procedure. In Experiment 2, presentation of either the hand or foot object (the prime) preceded the hand vibration (the target). The object prime was presented on the screen for the same duration as the vibratory prime in the previous experiments (250 ms) and was followed by either a hand vibration or no vibration. The same 6000 Hz tone as in Experiment 1 coincided presentation of the object prime. Participants were required to say 'yes' if they felt a vibration and 'no' if they did not feel a vibration as quickly and accurately as possible.

Results

All errors and spoils were removed prior to analysis (12.9% of the total trials). We conducted a 2 (Object [Hand Item, Foot Item]) x 2(Vibration [Hand Vibration, No Vibration])

general linear model ANOVA on median RTs. There was a significant main effect of Vibration, $F(1, 27) = 12.62$, $MSE = 838.79$, $p = .001$, $\eta_p^2 = .32$, whereas the main effect of Object was not significant, $F(1, 27) = .011$, $MSE = 680.92$, $p = .92$, $\eta_p^2 < .001$, suggesting that, unlike Experiment 1, there were no inherent differences in difficulty for responding based on the different object categories. Importantly, there was a significant Object x Vibration interaction, $F(1, 27) = 4.46$, $MSE = 537.26$, $p = .044$, $\eta_p^2 = .14$ (see Figure 11).
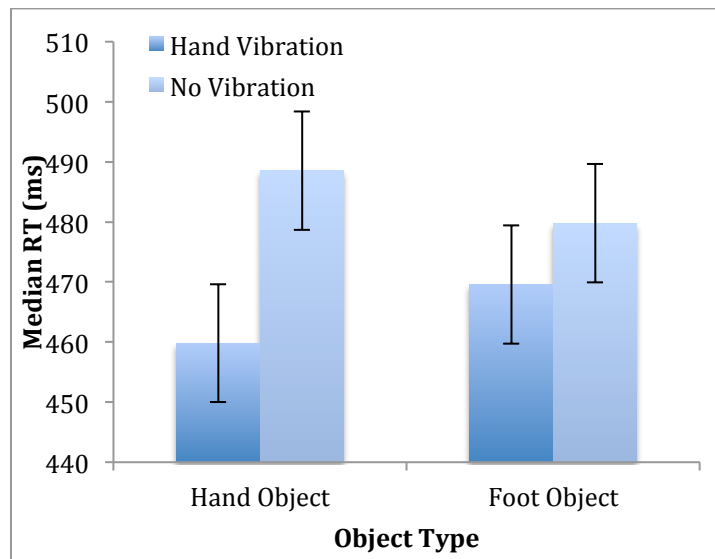
Figure 11. Median somatosensory detection RT (ms) of the hand vibration for the hand and foot objects. Error bars represent 95% confidence intervals (±9.85 ms); see Loftus and Masson (1994).

When examining percent error rates, there was no significant main effect of Object, $F(1, 27) = 1.64$, $MSE = 37.28$, $p = .21$, $\eta_p^2 = .057$, nor a main effect for Vibration, $F(1, 27) = 3.36$, $MSE = 51.33$, $p = .078$, $\eta_p^2 = .11$ The Object x Vibration interaction was not significant, $F(1, 27) = 1.27$ $MSE = 30.09$, $p > .25$, $\eta_p^2 = .045$. The means and standard deviations were $M = 11.02$, $SD = 5.09$ for the Hand Vibration Hand Object condition, $M = 13.67$, $SD = 9.42$ for the Hand Vibration Foot Object condition, $M = 9.71$, $SD = 7.77$ for the No-Vibration Hand Object condition, and $M = 10.02$, $SD = 6.56$ for the No-Vibration Foot Object condition (see Figure 12). Post-hoc t-tests indicated a potential speed-accuracy trade-off in the foot object condition, whereby there was a marginally significant difference between the Vibration and No-Vibration conditions for these objects. Specifically, participants appeared to be less accurate in the vibration condition than the no vibration condition, $t(27) = 2.02$, $p = .053$, $\eta_p^2 = .13$. No significant speed

accuracy trade-offs were present for the hand vibration hand object conditions, $t(27) = .82$, $p = .42$, $\eta_p^2 = .024$.
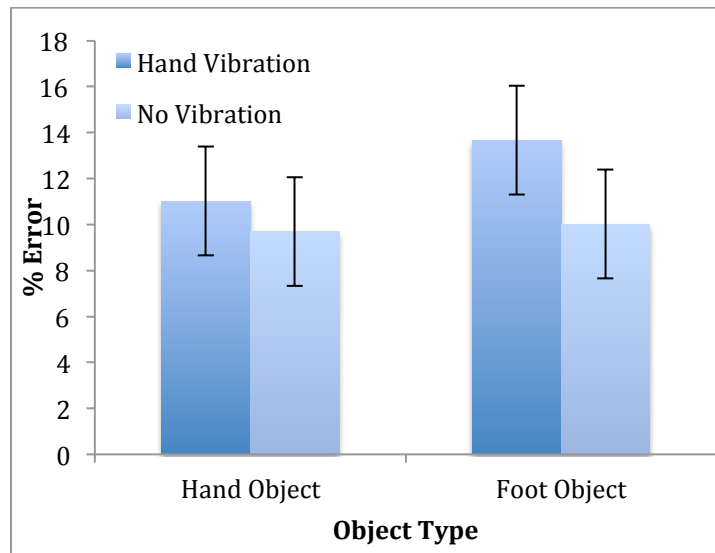
Figure 12. Percent error for somatosensory detection as a function of object type. There appears to be a significant speed-accuracy trade-off for the foot objects. Error bars ±2.37.

Planned paired t-tests on median RT between the hand object prime and foot object prime conditions were conducted for each object type. Results indicated that for the hand object primes, participants were significantly faster at detecting the presence of the hand vibration ($M = 459.82$, $SD = 77.92$) than when they were at detecting its absence ($M = 488.52$, $SD = 81.34$), $t(27) = -3.65$, $p = .001$, $\eta_p^2 = .33$. The foot object primes resulted in no significant differences between detecting the presence of the vibration ($M = 469.59$, $SD = 74.65$) versus its absence ($M = 479.82$, $SD = 76.21$), $t(27) = -1.69$, $p = .10$, $\eta_p^2 = .096$, however the 95% confidence intervals do indicate that there is a small but significant difference between these two conditions. As well, based on the 95% confidence intervals, the detection of a present vibration was significantly slower in the foot object condition than the hand object condition (however this did not reach significance using a paired t-test, $t(27) = -1.61$, $p = .12$, $\eta_p^2 = .087$).

Bayesian Analyses. Bayesian analysis examining priming effects in the hand items showed a Bayes factor of 28.05 in favour of an effect. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .97 in favour of the alternative hypothesis, providing strong evidence of an effect. The priming effects for the foot objects

resulted in a Bayes factor of 1.83 in favour of the null, and thus a posterior probability of 0.353 in favour of an effect. The Bayes factor for the Object x Vibration interaction was 1.09, resulting in a posterior probability of .53 in favour of the alternative hypothesis.

Once again, when examining ratings for interaction familiarity, the foot objects were found to be interacted with significantly less than the hand objects ($M = 5.21$, $SD = .54$ and $M = 2.52$, $SD = .41$, respectively), $t(27) = -34.25$, $p < .001$, showing a similar pattern to Experiment 2.

Discussion

Results from this experiment show a reciprocal relationship between object processing and the somatosensory system. Although the foot objects also showed faster 'yes' responses to the prime, this effect is most likely due to a well-known phenomena in psychological research that participants are generally faster at identifying that a stimulus is present than they are at reporting that a stimulus is absent (e.g., in object detection, Biederman, Glass, and Stacy, 1973). However, this bias would be apparent for both the hand and the foot objects and, thus the presence of the interaction becomes crucial for interpreting the results. As participants were faster at detecting the somatosensory prime when it was preceded by a hand object, and the degree of this facilitation differed significantly between the object types (as indexed by the significant Object x Prime interaction), it appears that the hand objects automatically evoked activation in the somatosensory system that subsequently facilitated detection time. Importantly, based on the 95% confidence intervals, detection of the target when the prime was a hand object was found to be significantly faster than when the prime was a foot object, further supporting this interpretation. Finally, the foot object results also appear to be compromised by a speed accuracy trade-off, thus suggesting that although the participants were significantly faster at detecting the hand vibration when it was preceded by a foot object, they made significantly more errors. This was not the case with the hand object primes, further supporting our conclusions.

It is important to note that in this experiment, the participants were not instructed to imagine themselves interacting with the prime object, and thus were not explicitly asked to draw upon semantic action knowledge of that object. This is an interesting finding, as it suggests that the hand objects *automatically* evoked sensorimotor programs in the absence of explicit instructions to do so. This is interesting in comparison to the results of Experiment 4, which found no effect of the somatosensory prime on object naming. However, we propose two possible explanations to this apparent difference. First, it may be the case that the visual information is

more salient than the somatosensory information, and therefore the participants are more able to ignore the somatosensory prime (Experiment 4) compared to the visual prime. This is in concordance with research by Buelte et al. (2008) who found applying repetitive TMS to virtually lesion the anterior IPS selectively impaired trials where the participants engaged in visual encoding of an object followed by a tactile recognition task, but not when they engaged in tactile encoding of an object followed by a visual recognition task. Thus, it follows that visual information may be more salient than haptic information, therefore leading to less influence of the somatosensory cue when it precedes object processing and more influence of the object prime when it precedes somatosensory detection. Alternatively, it may be the case that the context of the task in this experiment made it favourable for the sensorimotor representations of the objects to the drawn upon. Specifically, it is possible that in the context of a detection task, participants placed more weight on the object cue in order to perform the task as quickly as possible. This may help to explain the trend for a speed/accuracy trade-off seen in the foot object condition, as participants were more likely to say 'no' in the presence of a hand prime (i.e., greater percent error) when the foot object prime was presented than any other condition, suggesting that the foot object may have biased the participant to report that the hand prime was not detected. Regardless, this experiment provides further evidence for an intrinsic relationship between processing manipulable objects and the somatosensory system, as well as extending the aforementioned results to accommodate some level of automaticity of the sensorimotor representations evoked by viewing the object pictures.

Experiment 6

This Experiment will use a foot vibration target in place of the hand vibration target used in Experiment 5, in order to examine whether the nature of the object prime has the ability to aid sensory detection of the vibratory stimulus to the foot. Thus, this experiment is analogous to Experiment 3, which sought to examine whether the facilitatory effects in response to the hand prime were due primarily to matching processes, except with a similar procedure to Experiment 5.

Hypotheses

We hypothesize that, because the benefits of somatosensory priming were exclusive to the hand vibration in Experiments 1 and 2, there should be no impact of object type on detection of the foot somatosensory prime. Therefore, we expect to find no evidence of matching effects in this experiment, and therefore that the object type should not differentially speed detection of the foot somatosensory prime.

Methods

The methods and participants were the same as for Experiment 5, with the following exceptions.

Procedure. In this experiment, the hand vibratory prime was replaced with a foot vibratory prime (similar to Experiment 3).

Results

All errors and spoils were removed prior to analysis (13.9% of the total trials). We conducted a 2 (Object [Hand Item, Foot Item]) x 2 (Vibration [Foot Vibration, No Vibration]) general linear model ANOVA on median RTs. There was a significant main effect of Vibration, $F(1, 27) = 12.29$, $MSE = 1555.71$, $p = .002$, $\eta_p^2 = .31$, such that participants were faster at responding 'yes' in the presence of the vibration than responding 'no' in the absence of the vibration ($M = 461.56$ and $M = 487.70$, respectively). Similarly to Experiment 5, the main effect of Object was not significant, $F(1, 27) = .23$, $MSE = 714.39$, $p = .64$, $\eta_p^2 = .008$. Importantly however, unlike Experiment 5, there was no significant Object x Vibration interaction, $F(1, 27) = .62$, $MSE = 655.71$, $p = .44$, $\eta_p^2 = .022$ (see Figure 13). This indicates that the object category is not differentially influencing vibration detection.
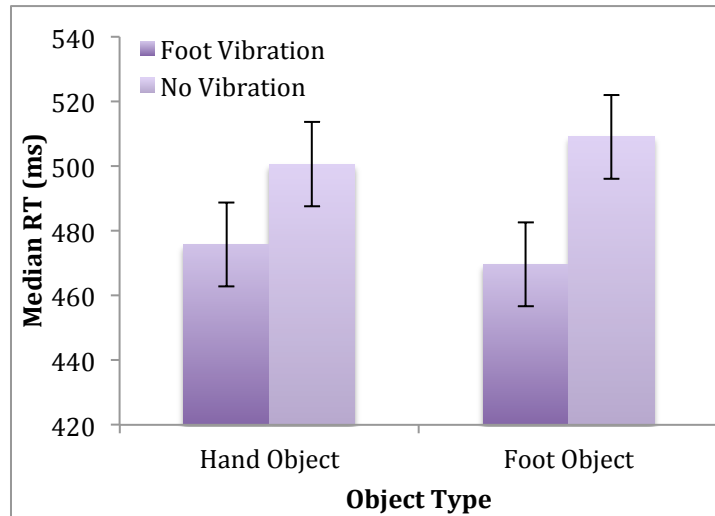
Figure 13. Median somatosensory detection RT (ms) of the foot vibration for the hand and foot objects. Error bars ±13 ms.

When examining percent error rates, there was a significant main effect of Vibration, $F(1, 27) = 6.74$, $MSE = 96.80$, $p = .015$, $\eta_p^2 = .20$. The main effect for Object was not significant, $F(1, 27) = 1.72$, $MSE = 26.32$, $p = .20$, $\eta_p^2 = .060$. The Object x Vibration interaction was not significant, $F(1, 27) = .53$, $MSE = 52.26$, $p = .47$, $\eta_p^2 = .019$. The means and standard deviations were $M = 12.24$, $SD = 10.00$ for the Foot Vibration Hand Object condition, $M = 12.51$, $SD = 10.43$ for the Foot Vibration Foot Object condition, $M = 6.42$, $SD = 5.67$ for the No-Vibration Hand Object condition, and $M = 8.69$, $SD = 8.05$ for the No-Vibration Foot Object condition (see Figure 14). Based on these results, it appears that there may be a significant speed accuracy trade-off, such that the faster 'yes' detection responses are compromised by increased errors.

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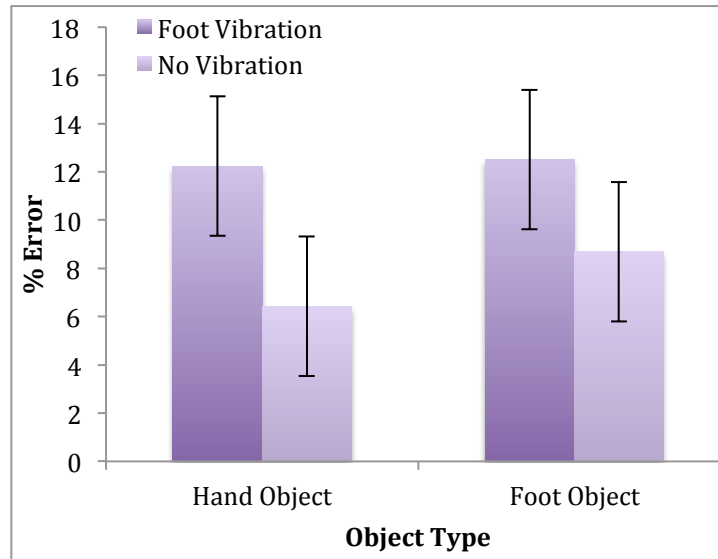
Figure 14. Percent error for somatosensory detection as a function of object type. There appears to significant speed accuracy trade offs in vibration detection for both object types. Error bars ±2.89.

Planned paired t-tests between the vibration and no-vibration conditions were conducted for each object type. Results indicated that hand object primes led to significantly faster detection of the vibratory prime ($M = 464.68$, $SD = 75.61$) than reporting the vibration's absence ($M = 487.00$, $SD = 62.90$), $t(27) = -2.63$, $p = .014$, $\eta_p^2 = .20$. Foot object primes also showed significant differences between detecting the presence of the vibration ($M = 458.45$, $SD = 72.31$) versus detecting its absence ($M = 488.39$, $SD = 72.14$), $t(27) = -3.24$, $p = .003$, $\eta_p^2 = .28$.

Bayesian Analyses. Bayesian analysis examining priming effects in the hand items showed a Bayes factor of 2.89 in favour of an effect. Assuming prior odds of one for the null and alternative hypotheses, we obtained a posterior probability of .743 in favour of the alternative hypothesis. The priming effect for the foot objects resulted in a Bayes factor of 10.71 in favour of the alternative hypothesis, and thus a posterior probability of 0.915 in favour of an effect. The Bayes factor for the Object x Vibration interaction was 5.08 in favour of the null, resulting in a posterior probability of .164 in favour of the alternative hypothesis. Ratings for interaction familiarity were the same as Experiment 5.

Discussion

The results from this experiment serve to provide a more comprehensive picture of the impact of object processing on somatosensory detection. Based on the results of Experiments 1

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and 2, we expected that the relationship between object processing and the somatosensory system was exclusive to hand objects and hand vibration, which is supported by the findings of this experiment. As the priming effects from the hand object primes were not shown to vary from the priming effects from the foot object primes, we have found no evidence to suggest that the nature of the object prime led to differentially faster foot vibration detection. Further, these results provide evidence that the pattern found in Experiment 5 is (similarly to Experiment 2) not due to matching processes between the object prime and the vibration target, as both the hand and foot objects showed a similar pattern of results. Overall, participants were significantly faster at detecting the prime when it was present as opposed to stating it was absent (congruent with the results of Experiment 5). However, this did not vary differentially based on the nature of the object prime (as indicated by the lack of a significant Object x Prime interaction) and thus the object prime did not influence somatosensory processing. As well, there was a significant speed-accuracy trade-off for target detection regardless of the object type, whereby although participants were faster at indicating that they detected the vibration, they were also less accurate. Overall, these results support our interpretation of the findings from Experiment 5 being due to an intrinsic relationship between the somatosensory system and hand object processing, rather than simple matching processes.

CHAPTER 5

GENERAL DISCUSSION

This series of experiments provides support for the idea that the conceptual representations of objects are in part encompassed in the somatosensory system, thus supporting theories of embodied cognition. Taken together, results from Experiments 1 and 2 provide direct evidence that at least part of the semantic representation of graspable objects involves the somatosensory system. As processing benefits were found for hand objects when the somatosensory system was primed, we have shown that these two processes share at least some underlying neural resources in the sensorimotor system. In contrast, the non-graspable (Experiment 1) and foot objects (Experiment 2) did not show processing benefits as a result of the prime, suggesting that the representation of these objects is *not* held within the sensorimotor areas associated with the hand. Importantly, based on the presence of the 6000 Hz tone at the onset of each of the trials, our results cannot be attributed to alerting effects, such that faster RTs in the vibration condition can be attributed to decreased temporal uncertainty (Callejas et al., 2005), which would lead to larger cuing effects in the faster hand object condition than the slower foot object condition.

Further, Experiment 3 provides evidence that these priming effects cannot be attributed to semantic matching, such that drawing attention to the hand aids processing of hand related objects, as this effect did not arise with the foot objects when using a foot prime. This suggests that the effects from Experiments 1 and 2 were due to the somatosensory nature of the prime, and not simply the prime itself. This experiment also suggests that general somatosensory activation (in this case, via the foot prime) is not sufficient to influence object processing, as the hand objects showed no processing benefits in the presence of the foot prime, and thus that conceptual representations have domain specific sensorimotor activation. Further, based on the ratings of interaction familiarity, it appears that prior experience with an object influences whether or not the conceptual representation of the object will be held in the sensorimotor system (in concordance with Kiefer et al., 2007; Weisberg et al., 2007; James et al., 2002), as the foot objects were shown to be interacted with significantly less than the hand objects. Thus, results from Experiments 1 to 3 support the conclusion that the somatosensory system has the ability to influence object processing in a way that is dependent upon prior action experience with the object.

The evidence provided from Experiment 4 has important implications for evaluating the sensorimotor involvement automatically evoked upon presentation of picture of an object. If simply viewing an object relies on the same neural mechanisms as those employed when performing the semantic generation task in Experiments 1 and 2, we would have expected to see a similar pattern of results in naming. This was not the case, however, as the somatosensory prime was not shown to impact object processing when participants were not required to access the action characteristics of the object. Thus, this experiment provides evidence that the semantic representation of objects can be accessed in more than one way, with different forms of access leading to differential involvement of the sensorimotor system (see also Borowsky & Masson, 1996 for an additional example where naming was not as effective at eliciting semantic effects compared to other tasks). It is important to note that although no effects of the somatosensory prime were found in this experiment, this does not necessarily indicate that there is no automatic sensorimotor activation. Indeed, the results from Experiment 5 provide evidence that there is some degree of automatic somatosensory involvement during object processing, as mere presentation of the hand object primes led to differentially faster detection of the somatosensory stimulus. In addition, the findings from this experiment further corroborate the findings from Experiments 1 and 2, providing converging evidence of a reciprocal relationship between the somatosensory system and the representation of manipulable objects. Finally, Experiment 6 examined how object processing influenced foot vibration detection, finding that somatosensory detection did not vary differentially as a function of the type of object prime. This provides further support that the reciprocal relationship between somatosensory and object processing is constrained to hand items and hand vibration. As well, the results from Experiment 6 showed that the results found in Experiment 5 were once again not due to matching effects between the prime and the target and, instead, that the manipulable nature of the object prime influenced somatosensory detection. Overall, this series of experiments serves to provide insight into the complex relationship between object processing and the somatosensory system. Implications of these findings for theories of embodied cognition will now be discussed.

Implications for Embodied Cognition

To begin, these results support theories of embodied cognition that posit that some, but not all, of the conceptual representation of objects are held in the sensorimotor systems associated with obtaining semantic knowledge of that object. This is in concordance with the

theories of Barsalou (2008) and Gallese and Lakoff (2005), which assert that semantic representations arise as partial simulations of the perceptual and motor information used in encoding. In addition, these results are in support of studies that have found a functional role of the sensorimotor system in object processing (e.g., Witt et al., 2010; Yee et al., 2013), as well as studies that have found differential sensorimotor involvement as a function of motor experience (e.g., Kiefer et al., 2007; Weisberg et al., 2007). Similarly to Witt et al. (2010), activation of the sensorimotor system (in this case, the somatosensory system) had the ability to influence object processing. While their study showed interference between naming manipulable objects while engaging in a motor task (indicating that processing the object required some of the same neural resources as performing the motor task), our results show that priming the somatosensory system *facilitates* processing. This is similar to the results obtained by Yee et al. (2013), who showed that haptic exploration of an object had the ability to facilitate the identification of degraded pictures of objects.

It is important to note that based on the nature of our task (which sought to maximize personally-relevant sensorimotor involvement) we are not arguing that viewing of pictures of objects inherently leads to *strong* sensorimotor system involvement (congruent with the findings of Bub & Masson, 2010 and Yu et al., 2014, who failed to replicate the results of Tucker & Ellis, 1998 and of Cant et al., 2005, who failed to replicate the findings of Craighero et al., 1996; see also Mahon & Caramazza, 2008, who purport that sensorimotor involvement is an automatic by-product of perception). Instead, we suggest that contextual and top-down processing cues can influence the degree of motor and sensory involvement (a conclusion that is supported by research examining embodiment of words; see Tomasino & Rumiati, 2013 for a review) and, therefore, that by having participants rely on their own subjective experience with a given object, maximal recruitment of sensorimotor areas would be an effective, top-down processing strategy. However, results from Experiment 5 provide evidence of at least some level of automatic somatosensory system involvement, as the hand objects were able to prime the somatosensory system in the absence of specific instructions to process the object. This has important implications for research investigating embodied cognition, as it suggests that some tasks are not optimal for examining the extent of sensorimotor system involvement. If the representation of an object can be accessed in a variety of ways, it becomes pertinent to understand the conditions by which embodiment can be most effectively assessed. Therefore, our research shows that semantic

generation is a valuable task that may be more sensitive to examining embodiment effects than standard naming paradigms, opening a new avenue of exploration to potentially subtle sensorimotor effects.

In line with this, our research also provides evidence that embodiment effects arise primarily as a result of mental simulation. As the semantic generation task used in Experiments 1 to 3 encouraged participants to draw upon their own action knowledge of how to interact with an object, we have optimized the likelihood that mental simulation will take place when processing the picture of an object. Thus, it can be inferred that because only the hand objects were influenced by the somatosensory prime, embodiment effects arise as a function of engaging in mental imagery with familiar objects. Further, the semantic generation task also maximized the probability that the participant would engage in *kinesthetic* mental imagery, whereby individuals imagine themselves performing the action from a first person perspective. This is important, as Stinear, Byblow, Steyvens, Levin, and Swinnen (2006) found that only this type of motor imagery modulated corticomotor excitability. As well, Ruby and Decety (2003) found that only kinesthetic motor imagery led to activation in the left IPL and the left SI (important areas in the human mirror neuron system). This provides further evidence that the task demands in these experiments were optimal for maximizing the amount of sensorimotor involvement elicited, thus allowing us to examine the extent to which action simulation and the somatosensory system interact.

Perhaps most importantly, our research draws attention to the relatively neglected contribution of *touch* to embodied cognition, which has been overshadowed by examinations of motor influences on object processing. Thus, this research begins to provide a more comprehensive picture of the nature of sensorimotor involvement in conceptual representation by elucidating the role of the somatosensory system during object processing in isolation of overt movements, such that objects that we have experience with are represented more strongly not only in the motor system (e.g., Kiefer et al., 2007), but also in the somatosensory system. As previous research has proposed convergence of information from all modalities to form conceptual representations (see Patterson, Nestor, and Rogers, 2007 for a review), our research provides bi-directional evidence for this claim in regards to the convergence of somatosensory information and object representation. This is in concordance with the research of Connell and Lynott (2010) and Ackerman et al. (2010) who have also shed valuable light on how sensory

contributions influence conceptual processing (in the domains of word processing and social judgments and decision making, respectively). Thus, in a broader context, our research supports theories that propose integrated and distributed representation of concepts throughout the mind, such that concepts consist of unified information from different modalities (see Patterson et al., 2007; in this case, the somatosensory system).

Implications for the Human Mirror Neuron System

This research also has important implications for extending our understanding of the human mirror neuron system. It is clear that the human mirror neuron system is undoubtedly more complex than the primate mirror neuron system, and while our understanding of this system in primates is quite comprehensive, there is still much to be learned about the nature of the mirror neuron system in humans. Neuroimaging research has thus far provided compelling evidence that, similarly to the monkey mirror system, the human motor system has mirror properties, as evidenced by the work of Cross et al. (2013) who, as discussed in the introduction, showed using fMRI prefrontal and inferior frontal activation in an imitation control paradigm. Similarly, Sartori et al. (2013) showed that the primary motor cortex also has mirror properties, as invoking reversible lesions to this area had the ability to modulate activity of the corticospinal tract in response to action observation. Further, this has been extended to the somatosensory system, as evidenced by the research of Avikainen et al. (2002), Hernandez et al. (2014), and Bisio et al. (2015), who all showed that the somatosensory system is involved in processing action information. Therefore, it may be interesting to examine whether there are a subset of mirror neurons that are activated both to somatosensation as well as motor observation, which would provide evidence of somatosensory mirroring. While the above research begins to shed light on how actions are represented in sensorimotor regions, as well as highlights the similarities between primate and human mirror systems, it does not address how conceptual representation may manifest itself in the mirror neuron system.

Ideally, examination of the mirror neuron system in humans would be investigated using electrophysiological recording (similar to primate models), however this currently cannot be performed in normal populations. Some recent studies have used clinical populations undergoing surgery to examine the mirror neuron system, specifically individuals undergoing surgery for intractable epilepsy. For example, Mukamel, Ekstrom, Kaplan, Iacoboni, and Fried (2010) used single neuron recording of the medial temporal and medial frontal cortex and found neurons that

were sensitive to both motor execution and observation. Similarly, Babiloni et al. (2016) used electrocorticography (in which an electrode grid is placed directly upon the cortex during brain surgery) to record brain activity of the primary somatosensory, primary motor, prefrontal, and premotor cortex of drug-resistant epileptic patients while the patients either executed or observed a movement. Their results found support for the existence of a human mirror neuron system, and that different regions contribute differentially during motor execution and observation, in order to allow for dissociation of 'self' versus 'other' actions. Because of the limited ability to perform electrophysiological recording of mirror neurons in humans, behavioural and neuroimaging studies provide invaluable information about the nature of action understanding and conceptual representation. This is especially important in regards to understanding how objects are represented in the mirror neuron system, as primates do not have the same understanding of the causal influence of an object for achieving a specific goal. Indeed, while primates appear to have the preliminary neural structures to integrate objects into the mirror neuron system (i.e., canonical and canonical-mirror neurons), the representation of objects in the primate mirror neuron system is highly dependent upon experience with the object and quite transient. Further, this does not extend to objects presented in extrapersonal space (Bonini et al., 2014), and presumably pictures of objects.

In light of this, the research presented in this thesis begins to shed light on the issue of whether pictures of objects are represented in the mirror neuron system- a phenomenon that, as of yet, has not been investigated using electrocorticography. Based on the results of Experiments 1, 2, and 5, we have shown that pictures of objects appear to initiate at least some level of action simulation, as evidenced by the somatosensory priming effects in Experiments 1 and 2, and more compellingly by the object priming effects in Experiment 5. Without direct instructions to do so, it appears that viewing the object picture automatically activated the somatosensory system in such a way that facilitated detection of the vibratory stimulus. As the somatosensory system has been shown to be a part of the mirror neuron system in humans (both independently and through its extensive connectivity with the motor cortex; Avikainen et al., 2002; Hernandez et al., 2014; Bisio et al., 2015), these priming effects suggest that presentation of picture of objects that have familiar action affordances can evoke mirror neuron system involvement. Thus, this research may serve to highlight some of the differences in complexity between the primate and human mirror system. Specifically, while both primates and humans have been shown to have canonical and

canonical mirror neurons that are active in response to three-dimensional objects presented in peripersonal space (e.g., Murata et al., 1997 and Grèzes et al., 2003, respectively), humans may also have a similar subtype of neurons that respond to the presentation of *two-dimensional* pictures of objects. Further, it is possible that this may be the mechanism by which the conceptual representation of objects becomes embodied, however future research is needed to explore this possibility.

Limitations and Future Directions

A particularly interesting avenue for exploration would be to have participants perform the same tasks using novel objects in a training paradigm. Similar to Kiefer et al. (2007), participants could be required to learn how to interact with novel, manipulable objects over a training period, whereby half of the participants had active motor experience interacting with it, while the other half have an equivalent amount of experience observing another individual interacting with it (this manipulation could also be performed within subjects, similar to our experiments). This would help to alleviate one of the limitations found in Experiments 1 to 4 such that there was significantly less variability in responses to the hand objects than to the non-graspable (Experiment 1) and foot objects (Experiments 2 to 4). This point is exemplified by a comparison of the results of Experiment 1 to Experiment 2, whereby the overall means show a similar pattern of results, however the critical interaction is not significant in Experiment 1. By reducing the variability in responding by introducing the foot objects, our task became much more sensitive to observing somatosensory priming interaction effects. While the substitution of the foot objects for the non-graspable objects significantly reduced response variability, there were still variability differences found between the foot and the hand items, most likely due to the participants' decreased familiarity with these objects. Thus, a training paradigm would serve to equate how familiar an individual is with how to interact with a specific object (either through observation or overt action), whereby the only difference between the groups would be action experience with the object. We predict that somatosensory priming effects would be much larger for the objects that participants had overt motor experience with in comparison to the objects that they did not interact with. By implementing a training paradigm, this task may become more sensitive to somatosensory priming effects, perhaps making it more sensitive in the naming condition to picking up somatosensory priming effects.

As well, in order to further test the conclusions drawn from this research, neuroimaging using these tasks is imperative. Currently, we are adapting these tasks for the fMRI environment in order to determine the locus of somatosensory priming effects on object processing. We predict that these two processes may overlap in the posterior parietal cortex, specifically the AIP and the anterior SMG, as these areas have been shown to be essential in tool processing (Orban & Caruana, 2014; Culham et al., 2004) and are in close proximity to the somatosensory cortex associated with the hand (see Figure 1). However, as stated above, these processes occur in a network of related brain regions, and thus electrocorticography may provide the most temporally and anatomically accurate picture of how and where these two processes may be interacting. Further, TMS may also provide valuable insight into these processes, as it allows for the possibility of selectively stimulating or inhibiting the hand somatosensory cortex. We would predict based on our results that when the somatosensory cortex is stimulated, hand object processing in the semantic generation task should be facilitated. Conversely, when the somatosensory cortex is inhibited, impairments in semantic generation would occur. This paradigm would be nearly analogous with the research presented in this thesis (with the somatosensory prime being replaced with the TMS pulse), and thus would provide important converging evidence for the presented effects. Thus, examining the neural mechanisms that underlie the results found in these experiments will provide valuable information into the nature of embodiment, as well as examining the possibility that the mirror neuron system is the mechanism for embodiment.

Another interesting future direction would be to study the implications of somatosensory stimulation for conceptual development and learning. The findings of Witt et al. (2010), who found interference between motor execution and conceptual processing of objects with congruent motor affordances, would suggest that motor system activation has the ability to impair conceptual processing, and thus interfere with conceptual development. However, throughout our experiments (as well as through evidence from Yee et al., 2013) it appears that somatosensory stimulation facilitates, rather than interferes with, conceptual processing. Therefore, it may be possible to integrate somatosensory stimulation during the acquisition of new concepts, in order to strengthen their subsequent representations. This would have important implications for learning, as it would provide a simple and cost effective way of integrating multisensory

information during the learning process, leading to more efficient semantic knowledge acquisition.

In line with this, another prospective application for this research is the potential for alleviating some of the perceptual deficits shown in those with autism. Dysfunction of the mirror neuron system has been proposed to play a critical role in the core behavioural deficits of autism spectrum disorder (see Oberman & Ramachandran, 2015). Although the majority of the research on perceptual deficits in autism has focused on face processing (see Golarai, Grill-Spector, & Reiss, 2008 for a review), previous research has also shown that these individuals have additional deficits in general object processing. For example, Blair, Frith, Smith, Abell, and Cipolotti (2002) found evidence for selective recognition memory impairments for objects that are capable of self-propelled motion (such as motorbikes and cats) relative to age-matched controls. Further, Behrmann et al. (2006) showed that individuals with autism were slower at discriminating between objects than controls (see also Behrmann, Thomas, & Humphreys, 2006 for a review). While more research is still necessary to determine the types of object stimuli that show the most impaired processing (as the object stimuli used in the aforementioned studies was quite limited), the possibility of strengthening conceptual representations using somatosensory stimulation during a training paradigm may serve to diminish some of these object-specific deficits.

Further, it may be possible to couple somatosensory stimulation with semantic generation of motor imagery in order to strengthen not only conceptual representation, but also aid in skill development and, potentially, rehabilitation. Somatosensory input from the environment is essential for motor learning and accurate motor task performance, based on the feedback that it provides to the motor system (Gentilucci, Toni, Daprati, & Gangitano, 1997; Rosenkranz & Rothwell, 2012; Pavlides, Miyashita, & Asanuma, 1993). Thus, it has been shown that reduced somatosensory function leads to decreased motor function (Rothwell et al., 1982), as well as disrupts recovery of movement after a stroke as occurred (Nudo, Friel, & Delia, 2000). In line with this, Ekstrand et al. (2016) provided evidence that integrating somatosensory stimulation into pre-surgical planning can improve surgical outcomes by helping to avoid disrupting somatosensory function. Interestingly, Rosenkranz and Rothwell (2012) showed that when participants performed a vibrotactile detection task (during which the participant was required to report when they detected a change in vibration frequency or the presence of a cutaneous stimulus), the somatosensory priming from this task increased plasticity of MC when they

engaged in subsequent motor execution. Thus, there is an intrinsic relationship between the somatosensory and motor systems such that the somatosensory system has the ability to influence the functioning and plasticity of the motor system.

In concordance with this, and similar to the semantic generation task used in these experiments, engaging in motor imagery has been shown to be a valuable tool in developing motor skills independent of actual motor execution. For example, Zijdewind, Toering, Bessem, Van Der Laan, and Diercks (2003) found that seven weeks of motor imagery training (whereby the participant imagined themselves repeatedly pointing their toe) had the ability increase the force exerted by the ankle muscles involved in performing this action in comparison to groups that did not engage in motor imagery. Similarly, research with clinical populations, such as individuals with stroke, spinal cord injury, and Parkinson's disease, has shown that engaging in motor imagery has the ability to aid in motor rehabilitation (see Stoykov & Madhavan, 2015 for a review). Further, research by Veldman et al. (2015) showed that modality specific somatosensory electrical stimulation has the ability to increase motor performance in normal populations of both the contralateral and ipsilateral limb in the presence of actual motor execution, as well as independently. Thus, our research has important implications for providing an effective and cost efficient paradigm for motor skill development in both normal and clinical populations through a combination of general somatosensory stimulation (via the vibratory stimulus) and semantic generation. This may be especially useful for patients with limited limb mobility who show impaired ability to engage in overt motor movements, as it may provide an alternative means of strengthening connectivity between the somatosensory and motor systems, in order to maximize motor recovery.

Our results may also have particularly interesting implications for examining individuals with object apraxia (i.e., individuals with impairments in their knowledge of how to interact with particular objects; see Stamenova, Roy, & Black, 2010). The existence of object apraxia has been presented as evidence that concepts are distributed across the sensory and motor domains, as this disorder results in a selective deficit in understanding the action semantics of objects. Of particular relevance, previous research has indicated that individuals with apraxia show impairments in drawing upon manipulation-based action information about objects (Lee, Mirman, & Buxbaum, 2014). When participants were asked to name an object in a visual display, apraxics showed abnormalities in the automatic activation of action information related to an object (in the

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form of delayed responses). Based on this, in our task it would be expected that individuals with apraxia would most likely show significant impairments in the semantic generation task in comparison to control participants, as retrieval of this action information would presumably be impaired. What is less clear however, is how the somatosensory prime may influence object processing in individuals with apraxia. As described above, the somatosensory system does not appear to interact with object processing in the same way that the motor system does, and thus it is possible that somatosensory stimulation may *facilitate* semantic generation performance of individuals with apraxia in a similar manner to which it facilitates performance in the participants in our study. This would suggest that while action representations of objects may be impaired in apraxia, somatosensory representations are not. Although this is currently speculative, research focused on how the somatosensory system is involved in conceptual processing in individuals with object apraxia will help to shed valuable light on the nature of semantic knowledge in both clinical and normal populations.

<div align="center">Conclusions</div>

To summarize, the importance of the present research is threefold. First, it extends theories of embodied cognition to accommodate somatosensory influences, such that the conceptual representations of objects that we interact with become integrated into not only the motor system, but also the somatosensory system. In line with this, we propose that the somatosensory priming effects shown in these experiments provide evidence of mirroring processes for pictures, suggesting that the mechanism by which concepts become embodied is based in the mirror system, thus providing a link between the mirror neuron system and the embodiment of conceptual representations. Second, in light of this, it expands our understanding of the human mirror system by providing evidence that picture processing (particularly semantic level processing) may also evoke mirror system involvement, as the somatosensory system has been shown to play an integral role in the mirror system (e.g., Avikainen et al., 2002) and object processing and somatosensory stimulation were shown here to interact. Third, and more broadly, this research elucidates the importance of research examining how *touch* and *somatosensation* contribute to cognition, which may have important applications for developing learning paradigms as well as exploring how somatosensation may be integrated with semantic generation tasks to aid in motor skill development and rehabilitation.

In conclusion, our results provide corroborative evidence that hand objects have sensorimotor representations that differ as a function of action experience, supporting theories of semantic representation that highlight convergence of modality-specific information, as well as theories purporting sensorimotor involvement in conceptual representations. Further, we also provide the first demonstration of a purely somatosensory influence on semantic processing of graspable objects, as well as the reciprocal relationship of object processing impacting somatosensory detection. It is important to note that while this evidence suggests that the somatosensory system is a *part* of object representation, that is not to say that the somatosensory system houses the *only* representation of that concept. In fact, our results further serve to highlight the complexities of object representation in the semantic system. By showing that the somatosensory system influences sensorimotor involvement in object processing and vice versa, we have provided a richer understanding of how objects are represented within our semantic system in such a way that accommodates somatosensory influences. We hope that this research will serve as the impetus for future experiments that continue to explore the characteristics and limits of somatosensory priming, as well as the contributions of other sensory modalities to object representation, in order to broaden our understanding of the mechanisms that underlie conceptual processing.

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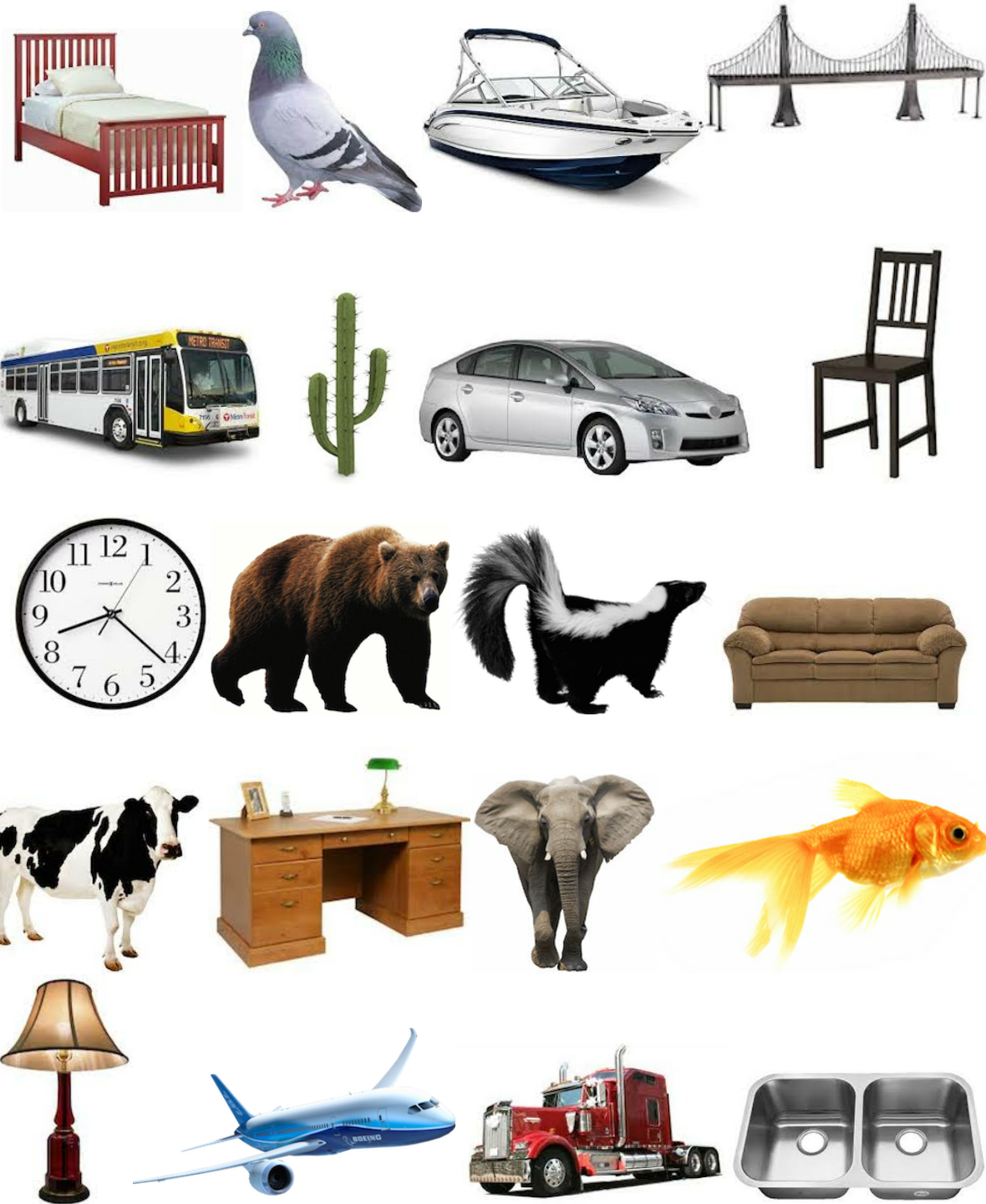
Appendix A

Graspable/Hand Objects

Appendix B

Non-Graspable Objects

Appendix C

Foot Objects