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Running Head: MOTOR RESONANCE AND NONCONSCIOUS MIMICRY

INVESTIGATING THE RELATIONSHIP BETWEEN MOTOR RESONANCE AND **NONCONSCIOUS MIMICRY**

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Bachelor of Arts, Psychology, Wilfrid Laurier University, 2009

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THESIS

Submitted to the Department of Psychology In partial fulfillment of the requirements for Master of Science, Cognitive Neuroscience Wilfrid Laurier University

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Abstract

Motor resonance refers to the mirroring of observed actions in one's own motor system. It is possible that motor resonance is the neural mechanism underlying nonconscious mimicry (NCM) - the ubiquitous phenomenon wherein people mimic the behaviour of interaction partners (Chartrand & Bargh, 1999). Previous research has shown that priming interdependent selfconstrual (interSC) increases mimicry (van Baaren et al., 2003). If motor resonance is the mechanism underlying NCM, then a manipulation known to facilitate mimicry (i.e. interSC) should increase motor resonance. In experiment one, we variably primed independent selfconstrual (indSC) - known to inhibit mimicry - and interSC in a motor priming paradigm. Participants observed videos of a hand squeezing a rubber ball hard or soft, which contained indSC and interSC prime words that changed colour to elicit a pre-instructed hard or soft squeeze response. The results indicated that when an observed action was incongruent with the required response, reaction time (RT) was slowed and electromyographic (EMG) activity was significantly modulated in the direction of the incongruence. Importantly, the RT cost and EMG modulation were significantly larger during the presentation of interSC primes. In experiment two, we used a more direct measure of motor resonance – motor-evoked potentials (MEPs) evoked with transcranial magnetic stimulation (TMS). Additionally, experiment two contained a dyadic interaction designed to elicit NCM at the beginning of the experimental session. Following the dyad, participants passively observed the same action videos used in experiment one, which contained interSC, indSC, or no prime words. Whilst participants observed the videos, MEPs were induced in the primary muscle underlying the action. The results from experiment two displayed a moderate positive correlation between NCM and motor resonance, as well as a significant effect of self-construal priming on MEP amplitude. Overall, the results

from experiments one and two converge to show that activating interSC induces hyper-motor resonance (and in fact, priming indSC induces hypo-motor resonance). Since interSC is also known to increase mimicry, our findings empirically link motor resonance and NCM. To qualify this statement, however, we found only a moderate correlation between mimicry and motor resonance in experiment two, suggesting that motor resonance, in the absence of social information, may not be enough to elicit mimicry on its own. Rather, in line with the social psychological literature on NCM, it is likely that a host of social, cognitive, affective, motivational and attitudinal factors combine with the basic motor resonance system to produce mimicry.

Keywords: Mirror neurons, Motor resonance, Action observation, Nonconscious mimicry, Chameleon effect

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Table of Contents

Abstract	3
Keywords	4
Acknowledgements	5
Table of Contents	6
General Introduction	8
Mirror Neuron System.	8
Primate evidence	8
Human evidence	9
Social Psychology Background	12
Nonconscious mimicry (NCM)	12
Self-construal and NCM	13
Theories of Mimicry	15
Cognitive Neuroscience Background	17
Motor-evoked potentials	17
Motor Priming	18
Experiment one	21
Introduction	. 21
Methods	22
Results	24
Discussion	29
Experiment two	31
Introduction	31

MOTOR RESONANCE AND... viii

Methods	32
Results	36
Discussion	39
General Discussion.	41
References	45
Figure Captions	53
Table Captions	55
Figures	56
Tables	67

General Introduction

When arguing with a "hand-talker," you are more likely to use gestures to get your point across. Conversely, when you have the same debate with a less animated partner, you will be less likely to use gestures to win the argument. The tendency of humans to mimic those we interact with has been called the Chameleon Effect, and will be referred to henceforth as nonconscious mimicry (NCM) (Chartrand & Bargh, 1999). The present paper describes research that employs neuroscientific methodologies to investigate NCM, with the goal of helping to answer the following question: what brain mechanism(s) make humans behave like chameleons?

Mirror Neuron System

Primate Evidence

In the early 1990's, researchers at the University of Parma made a serendipitous discovery while recording the activity of single neurons in a rostral area of the macaque premotor cortex, known as F5. It had previously been established that F5 cells discharge during the execution of specific motor acts, such as grasping, holding and manipulating objects. Furthermore, some F5 cells also discharged in response to visual stimuli congruent with the cells' motor properties, which were entitled *canonical neurons* (Rizzolatti et al., 1988). However, experiments by di Pellegrino and colleagues (1992) revealed that the canonical neurons were not the only F5 cells that displayed visuo-motor properties. During a recording session in which the research team was attempting to isolate movement-related neural activity in F5, it was incidentally noted that occasionally an experimenter's actions, such as executing a transitive grasping movement, activated a reasonably large proportion of neurons in the absence

of any overt movement from the monkey (di Pellegrino et al., 1992). The moniker *mirror neurons* was given to this population of F5 cells that were not purely motor, not responsive to the sight of actionable objects, but instead discharged during both the execution of motor acts and the passive observation of similar acts performed by another individual (Gallese et al., 1996). And, since their discovery, mirror neurons have burgeoned into a dominant research topic in psychology and the neurosciences.

Human Evidence

Mirror neurons allow the monkey to form an internal representation of and understand motor acts executed by others (Jeannerod, 1994; di Pellegrino et al., 1992). Humans are intensely social beings, and the importance of how we represent the actions of others made a human homologue of the monkey mirror neuron system a prime target for research. Neural intervention and functional neuroimaging studies have provided strong evidence for a mirror system in the human brain (Iacoboni, 2005).

An influential TMS study by Fadiga and colleagues (1995) found that participants displayed phasic motor facilitation during the passive observation of motor acts executed by the experimenter. Fadiga et al. (1995) delivered single-pulses of transcranial magnetic stimulation (TMS) over left primary motor cortex to elicit motor-evoked potentials (MEPs) from the first dorsal interroseus (FDI) and opponens pollicis (OP) muscles of the participants' right hand. When participants observed the experimenter grasp an object, both the FDI and OP showed enhanced MEP size, which was evidence of mirror activity, since both muscles would also be involved in the execution of a grasping movement. More conclusive, though, is the finding that FDI, but not OP, showed enhanced MEPs during the observation of a whole arm movement,

which would have been the same pattern of excitation had the participants been executing the movement themselves (Fadiga et al., 1995). Therefore, the participants' motor system was not only activated by the passive observation of another individual's movements, but the activation was strictly congruent with the types of movements observed, providing evidence of a mirror mechanism similar to the one described in the monkey.

In addition to the TMS evidence, several functional neuroimaging studies have suggested the presence of a mirror mechanism in humans (e.g. Rizzolatti et al., 1996; Iacoboni et al., 1999; Buccino et al., 2001). Whereas the precise temporal resolution of TMS can afford certain discoveries, for instance the phase-specific nature of motor facilitation during action observation (Gangitano et al., 2001), it does not allow researchers to precisely localize the cortical areas and neural circuits involved in action observation (Rizzolatti & Sinigaglia, 2008). Comparative architectonic analysis has shown that Brodmann area 44, or pars opercularis of the inferior frontal gyrus (IFG), can be considered the human homologue of premotor area F5 of the monkey (Petrides & Pandya, 1997). Thus, if a mirror system analogous to the monkey is to be found in the human, IFG represents a critical region of interest. A recent study by Kilner and colleagues (2009) used a functional magnetic resonance imaging (fMRI) adaptation paradigm to show cross-modal repetition suppression in IFG. Adaptation paradigms make inferences based on the fact that as stimuli that evoke activity in a given neuronal population are repeated, neural activity is reduced (Grill-Spector et al., 2006). In Kilner et al's (2009) study, participants either observed or executed two different grip actions, presented as sequential pairs of unimodal (i.e. executeexecute, observe-observe) and cross-modal (i.e. observe-execute, execute-observe) action stimuli. The key contrast for statistical analysis was repeated cross-modal presentation of the same actions versus repeated cross-modal presentation of different actions, with the hypothesis

that the former would lead to reduced activity in IFG. It was found that IFG activity was suppressed both when an executed action was followed by the same, rather than a different, observed action, and when an observed action was followed by the same, rather than a different, executed action (Kilner et al., 2009). Therefore, this study provides strong evidence that mirror neurons exist in IFG, which is the human homologue of monkey area F5.

The degree of functional congruence between the mirror neuron system in the monkey and the purported human version has been called into question (e.g. Hickok, 2009), however, what is clear from the human literature is that a similar cortical network involved in action execution is also activated during action observation. Henceforth, "motor resonance" will refer to the mirroring of observed actions in one's own motor system. It is now apparent that the motor resonance system plays an integral role in social cognition, with research implicating human mirror areas in action understanding (i.e. Fazio et al., 2009), imitation (i.e. Iacoboni et al., 1999) and empathy (i.e. Schulte-Rüther et al., 2007). With respect to imitative behaviours, it has been hypothesized that the motor resonance system is a viable mechanism underlying NCM – the ubiquitous phenomenon wherein people tend to non-consciously and unintentionally mimic the bodily movements, expressions, speech and gestures of interaction partners (Iacoboni, 2005; Iacoboni, 2009). Motor resonance is an intuitive mechanism for explaining how NCM occurs: when an interaction partner crosses their legs, it activates an internal motor representation for leg crossing in the observer, and once this externally triggered motor representation reaches threshold, mimicry occurs. However, despite this intuitive appeal of motor resonance as the neural substrate for NCM, there is a dearth of empirical support. This is perhaps due to the fact that NCM and the neural mechanisms involved in action observation have been studied by different groups of researchers (social psychologists and cognitive neuroscientists respectively).

In the following sections, I will elaborate on NCM, describing various aspects of the phenomenon that are pertinent to the present research, and outlining a prominent conceptual account for mimicry. Next, I will turn to some of the methods used in cognitive neuroscience to probe the nature of the motor resonance system, namely: MEPs and motor priming paradigms. Then, I will turn to the present research, and provide details of experiment 1 and 2 respectively. Lastly, I will discuss the contribution that the present research makes to the literature on mimicry and motor resonance.

Social Psychology Background

Non-conscious Mimicry

Human beings are an inherently social species. NCM is a low cost strategy that allows individuals to establish and maintain harmonious relationships with fellow group members (Lakin et al., 2003). The benefits of NCM are consistently evidenced in the social psychological studies on the phenomenon (for a review, see Chartrand & van Baaren, 2009). In addition, functional neuroimaging data has shown that the neurobiology of being mimicked is similar to that of receiving primary reward (Kühn et al., 2010).

Early mimicry research employed naturalistic observation to document posture sharing during a social interaction (e.g. La France & Broadbent, 1976). However, naturalistic observation studies provided a correlative (i.e. was leg-crossing coincidentally concomitant) rather than causal test of mimicry (i.e. did person 1's leg-crossing cause an increase in person 2's leg-crossing). To display causal mimicry, Chartrand and Bargh (1999) systematically manipulated behaviours displayed by a confederate during a dyadic interaction with participants.

The results from this study showed that participants displayed a significantly higher number of the target behaviours and facial expressions while the confederate was performing them, after controlling for baseline measures. A debriefing session indicated that participants were unaware of their mimicry. In a follow-up study, Chartrand and Bargh tested whether or not mimicry facilitated liking and rapport during the interaction. In this study, the confederates mimicked the behaviour of the participants in one group and maintained a neutral posture for another group. After the interaction, a questionnaire was administered, and results differed significantly between the mimicked and neutral group, with participants who were mimicked reporting a significantly higher degree of rapport and liking for the confederate. Lastly, in their third study, Chartrand and Bargh (1999) showed that individual differences in empathy covaried with individual differences in mimicry. Collectively, these studies confirm that people exhibit mimicry nonconsciously during an interaction with strangers, that mimicry facilitates liking and rapport, and that empathic individuals are more likely to mimic.

Since the finding of a relationship between empathy and NCM, priming methods have shown mimicry to increase as a function of a number of moderating variables, for example: the desire to affiliate (Lakin & Chartrand, 2003), high self-monitoring (Cheng & Chartrand, 2003), interdependent self-construal (van Baaren et al., 2003), positive mood (van Baaren et al., 2006) and as a response to social exclusion (Lakin et al., 2008). Of particular relevance to the present research is the finding that behavioural mimicry varies as a function of self-construal (van Baaren et al., 2003).

Self-Construal and NCM

Traditionally, psychological research has characterized the 'self' according to the traditional western view, that the individual is an independent, self-contained and autonomous entity. However, according to Markus and Kitayama (1991), the notion of the self as an entity detached from social context is untenable. To resolve this misguided convention, they used the term 'self-construal' to differentiate the interdependent self, which accentuates the influence of *others* on the self-schema (Markus & Kitayama, 1991). Although different cultures display a proclivity toward a given self-construal, with eastern cultures tending toward an interdependent self-construal (interSC) and western cultures toward an independent self-construal (indSC), research indicates that both types of self-construal can coexist within the individual. For example, Kühnen and Hannover (2000) variably primed interSC and indSC in the same participant and reported an increase and decrease in self-other similarity ratings, respectively. Since an interSC enhances perceived closeness and similarity between the self and others, it is probable that it would also enhance the similarity of behaviour displayed by interaction partners. In other words, interSC should facilitate NCM.

In order to determine whether self-construals affect NCM, van Baaren and colleagues (2003) exposed participants to self-construal priming (Kühnen & Hannover, 2000) prior to examining mimicry in a subsequent interaction with the experimenter. During the priming session, participants completed a scrambled sentence task, where they were given five words in nonsensical order and asked to respond by writing them as a grammatically-correct four-word sentence. The words included in the scrambled sentence differentiated the conditions, with one group subjected to interSC (i.e. together, integrate) and another to indSC (i.e. alone, mine) priming. A third group of participants was not primed (control condition). After the priming session, the participants rated music fragments while the experimenter wrote down their

responses. During the music-rating task, the experimenter played with his pen five times per minute. The data from this study showed that participants in the independent-self condition mimicked the pen playing behaviour significantly less than the control condition, whereas participants in the interdependent-self condition mimicked the behaviour significantly more than the control condition. Thus, activating interSC increases mimicry and activating indSC decreases mimicry.

Thus, mimicry is a low cost strategy used by humans to establish and maintain harmonious relations with other group members (Lakin et al., 2003). It can influence and is subject to the influence of a broad array of social, cognitive, affective, motivational and attitudinal moderators (see Chartrand & van Baaren, 2009). Understanding the social function of mimicry and its moderators, intriguing as it may be, still leaves one with important questions including: why do we mimic?

Theories of Mimicry

Early theories of mimicry asserted that it was a nonverbal communicative behaviour, used to make it known to our interaction partners that we understand and empathize with them (Bavelas et al., 1986). However, in their seminal study, Chartrand and Bargh (1999) showed that mimicry occurs under minimal conditions: without conscious awareness and among strangers with no goal to affiliate with one another. Additionally, more recent research methods have shown mimicry displayed by individuals in isolation, watching a videotaped model (e.g. Lakin & Chartrand, 2003, van Baaren et al., 2007). Thus, although mimicry may have evolved as a means of facilitating communication and promoting survival through socialization, the evidence that it

occurs among strangers and in isolation suggests a more basic reason for mimicry that goes beyond its communicative function (Lakin et al., 2003; Chartrand & van Baaren, 2009).

Perception-Behaviour Link

At the conceptual level, social psychologists have hypothesized that a direct perception-behaviour link could underlie mimicry. In this framework, an interaction partner's behaviour activates a perceptual representation, which automatically triggers a corresponding behavioural representation and, given the myriad social benefits of mimicry, the activated behavioural response is frequently to produce a matching motor output (Dijksterhuis & Bargh, 2001). The notion of a direct perception-behaviour link is compatible with the enduring ideomotor theory of action. According to ideomotor theory, actions are represented in the form the sensory feedback they produce. Thus, observing another individual acting automatically activates the corresponding motor plan (Greenwald, 1970; Brass & Heyes 2005; Brass & Spengler, 2009). Hence, at the conceptual level, the perception-behaviour link and ideomotor action plausibly account for NCM.

Motor Resonance

To form an adequate theory of NCM requires moving beyond a purely conceptual understanding, and elucidating the neural mechanisms underlying mimicry. In agreement with the suggestion of a direct perception-behaviour link, research in cognitive neuroscience is accumulating evidence that action perception and execution consistently employ a common network of cortical areas, also known as motor resonance. It has been hypothesized that motor resonance is a viable mechanism subserving imitation in general, including its non-conscious

form (i.e. NCM) in particular, as action observation leads to activation of the same brain areas that are employed during the production of a matching motor output (Iacoboni, 2005; Iacoboni, 2009; Chartrand & van Baaren, 2009).

Cognitive Neuroscience Background

In the cognitive neuroscience literature, action observation tasks are frequently used to investigate the motor resonance system. From this literature there are two types of methods frequently used to operationalize motor resonance: MEPs elicited using TMS and motor priming, indexed by reaction time (RT) and more recently, in some work from our laboratory, electromyography (EMG, Obhi & Hogeveen, 2010). Prior to describing the present research, the TMS induced MEP, and motor priming paradigms will be considered in turn.

TMS induced Motor-Evoked Potentials (MEPs)

The work of Penfield and Boldrey (1937) outlined a homunculus of anatomical representations in the primary motor cortex. When TMS pulses of sufficient intensity are delivered to a particular location on the homunculus, it evokes a descending corticospinal potential, which generates excitatory postsynaptic potentials (EPSPs) at the spinal motoneurons causing them to fire and resulting in an involuntary muscle contraction in the corresponding muscle, which can be recorded by EMG (Houlden et al., 1999). The resulting activity in the EMG trace is an MEP. If corticospinal excitability is high, the resulting MEP will be significantly larger than if corticospinal excitability is lower (Pascual-Leone et al., 1998). In motor resonance studies using MEPs, TMS stimulation intensity is held constant across baseline

and action observation conditions. Hence, increased MEP size during passive action observation is direct evidence of motor resonance.

Motor Priming

In motor priming paradigms, participants are exposed to action stimuli that are either congruent or incongruent with a to-be-executed response. The consistent finding is that action observation reliably modulates (the speed of) action execution. Specifically, observation of movements that are compatible with the response facilitates action execution, whereas observation of incompatible movements interferes with action execution. Facilitation of a response identical to one being observed is indirect evidence for motor resonance. For example, Brass, Bekkering and Prinz (2001) used a direct priming procedure to show that when participants observe a finger movement it facilitates faster execution of a compatible movement (e.g. observe finger lift, produce finger lift), but delays execution of an incompatible movement (e.g. observe finger lift, produce finger tap). Incidental motor priming has also been shown to modulate action execution. Incidental priming refers to situations in which the primed item or feature is completely task-irrelevant, suggesting that the effect cannot be wholly tied to an explicit cognitive strategy (Costantini et al., 2008). Bach and Tipper (2007) showed that when participants were shown a video of an actor kicking a ball, they were faster to identify the actor when they used a foot-response (congruent condition) than when they used a hand-response (incongruent condition) on a subsequent facial recognition task. The opposite result was observed when the actor was shown typing in the video. Thus, even though actions performed in the video stimuli were completely irrelevant during the identification task, effector priming emerged.

Recently, Obhi & Hogeveen (2010) added to the motor priming literature by asking whether different extents of an action made by a particular effector, and involving the same muscle groups, would result in priming that was specific to the extent of the observed movement. Participants held a rubber ball under an occluder and made hard or soft squeezes in response to colour cues that were super-imposed on videos depicting hard or soft squeezes of an identical rubber ball, whilst EMG activity in the abductor pollicis brevis (APB) and first dorsal interosseous (FDI) was recorded. Our results indicated that when the observed movement was incongruent with the cued response (i.e. observe hard, produce soft), response time (RT) was slowed and electomyographic (EMG) activity in the APB muscle was influenced in the direction of the incongruence between the video and the instructional cue (i.e. if observing a hard squeeze video during the execution of a soft squeeze response, that response would be more intense than during the observation of a soft squeeze video). Hence, task-irrelevant videos of an action modulated not only the speed with which a response was made, but also the physical characteristics of the instructed response. Specifically, the physical characteristics of the response became more similar to the response being depicted in the video.

If observation of a rubber ball being squeezed facilitates execution of a congruent response but slows production of an incongruent response, then it can be inferred that observation causes some increase in activation levels of the motor representation for the specific squeezing action observed. This "observation driven" activation *is* motor resonance. Hence, the interference caused by an incongruous observed action, or, conversely, the facilitative effect of a congruous observed action, make motor priming an indirect method for studying motor resonance.

Experiment One

In press with Cognitive Neuroscience as:

Hogeveen, J. & Obhi, S. S. (2010). Altogether now: Activating interdependent selfconstrual induces hyper-motor resonance

Introduction

The studies outlined in this thesis seek to provide empirical support to the claim that motor resonance underlies NCM, or at least that the two phenomena are fundamentally linked. If motor resonance causes behavioural mimicry, or is a lower level manifestation of the same phenomenon, it should be affected by factors that are known to moderate mimicry. Many factors have been found to moderate NCM, including the nature of an individual's self-construal (van Baaren et al., 2003). In experiment one, participants engaged in a motor priming paradigm akin to a previous study from our laboratory (Obhi & Hogeveen, 2010). In the original version of the experiment, colour dot stimuli were used to cue responses. However, in experiment one, coloured independent and interdependent self-construal prime words were used to cue responses. We hypothesized that interSC words would be associated with a significantly larger motor priming effect than indSC words. If interSC or indSC activation, which are known to moderate NCM, also moderate motor priming, this would support the notion that the two behavioural phenomena are mediated by the same motor resonance system. However, it is important to state that such a result does not prove beyond doubt that motor resonance underlies NCM, because, in

principle, two independent processes could be similarly affected by a common experimental variable.

Methods

Participants

12 participants (7 male, 5 female, between the ages of 18 and 24) took part in the experiment for partial course credit. All participants had normal or corrected-to-normal vision and all but two were right-handed. The experiment conformed to local ethical guidelines and informed consent was obtained from all participants.

Apparatus and Stimuli

The experiment was programmed using Superlab v.4 (Cedrus Corporation, San Pedro, California) and run on a Dell desktop computer with stimuli displayed on a 20" LCD monitor. EMG data was recorded from the APB muscle using a Biopac psychophysiological recording system, with pairs of surface electrodes placed in a belly tendon arrangement over the APB muscle of the participant's right hand. The EMG signal was acquired with a 1KHz sampling rate, amplified (to 5.0 mV) and filtered (band pass 10-500Hz), and sent to a laptop computer for offline analysis.

Experimental stimuli were videos depicting a right hand (palm facing down) squeezing a rubber ball between the thumb and index finger hard, such that the rubber ball was substantially deformed, or soft, such that the rubber ball was minimally deformed. The videos consisted of a single squeeze repeated either two or three times. Word cues were superimposed in black font

throughout the videos, but changed colour to blue or yellow between either the first and second (2-squeeze video) or the second and third (3-squeeze video) squeezes. The colour change prompted a hard or soft squeeze response from participants, according to a pre-instructed colour-response mapping. The colour-response mapping was reversed for half of the participants to eliminate any colour-specific effects. Video-editing was performed using Final Cut Express v.4 (Apple Corporation, Cupertino, California).

The list of independent and interdependent self-construal primes was adapted with permission from Kühnen and Hannover (2000), the same source used by van Baaren et al. (2003). Prior to finalizing the word lists, a lexical decision task tested for RT differences between the interdependent and independent words. Paired-samples t-tests revealed no significant difference in RT (all p > .05). None of the participants from the lexical decision task took part in the experiment proper. The complete word lists adapted from van Baaren et al. (2003) are given in Table 1. After the study was complete, participants were asked whether they noticed the changing intensities of the observed movement.

Design and Procedure

The experiment contained three within-subjects factors: video type (hard or soft squeeze), cue type (hard or soft squeeze), and word type (independent or interdependent self-construal primes). Thus, there were four video-cue congruent and four video-cue incongruent experimental conditions (Figure 1 shows the conditions and sample stimuli). Each participant was exposed to four randomized blocks, each containing 20 congruent hard squeeze trials (10 of each word type), 20 incongruent hard squeeze trials (10 of each word type), 20 congruent soft squeeze trials (10 of each word type) and 20 incongruent soft squeeze trials (10 of each word type). In addition,

each block contained 60 catch trials that did not require a response. Catch trials contained the same video stimuli as response tials, with a green cross presented in place of the word colour change.

Throughout the experiment, participants rested their hands in a neutral position (midway between supinated and pronated) on a pillow located in front of the monitor displaying stimuli. Once comfortable in this set-up, the participant's hand was covered with a box that was draped with black fabric to occlude vision of their hand, such that the only visual input was from the monitor. Each trial began with a black fixation cross that appeared on a white screen for 500 ms. Following the fixation cross, a video from one of the eight experimental conditions was presented. Videos depicted either a hard or soft squeezing action, with an interdependent or independent prime word in black text superimposed. For both hard squeeze and soft squeeze videos, the word changed to one of two colours (blue or yellow), which prompted participants to respond with a pre-instructed squeeze action. Videos showed either two squeeze repetitions or three squeeze repetitions, which were chosen due to time constraints, and the finding that video length does not significantly modulate congruence effects in our motor priming paradigm (Obhi & Hogeveen, 2010). For videos showing two squeezes, word colour change occurred 1100-1260 ms after video onset, whereas for three squeeze videos it occurred 2090-3050 ms after video onset. In response to the word colour change, participants made either a hard or soft squeeze of the ball they were holding, according to the pre-instructed colour-response mapping. In all conditions, participants were given 2000 ms to respond before the next trial started with representation of the fixation cross. Responses were executed using a rubber ball similar to the one used in the videos.

Results

Errors and Outliers

Data from all 12 participants were processed and subjected to inferential statistical analysis. Trials where the APB displayed activation prior to the cue onset, or where the RT was greater than or less than 3 standard deviations from the mean, were omitted from the overall analysis. This procedure resulted in removal of 3.14% of the data.

Analysis Procedures

To establish the effect of our independent variables on the dependent measures of RT and APB EMG, the means for each condition were entered into a 2 (cue type: hard or soft) x 2 (video type: hard or soft) x 2 (prime type: independent or interdependent) repeated-measures ANOVA. In view of the fact that we had clear a priori directional predictions based on previous work (e.g., Obhi & Hogeveen, 2010; van Baaren et al, 2003) we also performed a series of planned one tailed paired-samples t-tests.

Reaction Time

Reaction time (RT) was determined as the time between the onset of the colour cue and the onset of the EMG burst underlying the response. There was a significant main effect of cue type ($F_{1,11} = 35.504$, p < .001) and prime type ($F_{1,11} = 5.504$, p = .039). The video type factor did not reach statistical significance ($F_{1,11} = 3.327$, p > .05). There was also a significant cue type x video type interaction ($F_{1,11} = 29.29$, p < .001). A paired-samples t-test showed that participants were significantly faster to respond when the cue instructed a hard squeeze and the video showed

a hard squeeze (congruent condition, hard: 493 ms) than when the cue required a hard squeeze and the video showed a soft squeeze (incongruent condition, hard: 567 ms, $t_{11} = 6.275$, p < .001). Another paired-samples t-test showed that participants were significantly faster to respond when the cue instructed a soft squeeze and the video showed a soft squeeze (congruent condition, soft: 577ms) than when the cue instructed a soft squeeze and the video showed a hard squeeze (incongruent condition, soft: 618 ms, $t_{11} = 2.685$, p = .011). These results replicate the findings from our previous study, showing that RT varies as a function of the congruence between the observed and executed squeeze (Figure 2).

There was also a significant cue type x video type x prime type interaction ($F_{1.11}$ = 12.269, p = .005). A paired-samples t-test showed that when the colour cue instructing a hard squeeze was also an interdependent prime and the video showed a hard squeeze (interdependent congruent condition, hard: 486 ms), participants were significantly faster to respond than when the video showed a soft squeeze (interdependent incongruent condition, hard: 586 ms, t_{11} = 6.19, p < .001). A second paired-samples t-test showed that when the colour cue instructing a soft squeeze was also an interdependent prime and the video showed a soft squeeze (interdependent congruent condition, soft: 568 ms) participants were significantly faster than when the video showed a hard squeeze (interdependent incongruent condition, soft: 634 ms, t_{11} = 3.403, p = .003). Two more paired-samples t-tests compared the equivalent conditions for the case when the colour cue was also an independent prime. A significant difference was found between the independent congruent hard condition (493 ms) and the independent incongruent hard condition (548 ms, t_{11} = 3.544, p = .003). No significant difference was found between the independent congruent soft condition and the independent incongruent soft condition (p > .05).

To directly compare the impact of the interdependent and independent primes on congruence effects, we calculated the difference between congruent and incongruent conditions for each prime type. Paired samples t-tests showed that the difference between congruent and incongruent conditions was significantly larger for interdependent primes than independent primes (interdependent incongruent minus congruent, hard: 100 ms vs independent: 47 ms, t_{11} = 2.905, p = .007; interdependent incongruent minus congruent, soft: 66 ms vs independent: 17 ms, t_{11} = 3.048, p = .006 – Figure 3).

To determine whether participants were aware of the video-cue congruence after the experiment each participant was asked whether they had noticed any changes in the observed squeezing movement across trials. One third of participants (n=4) reported that they were unaware of any differences in the observed movement across trials. We conducted an additional set of planned comparisons using only data from this 'naïve' group of participants. As can be seen in table 2, this analysis revealed an identical pattern of results as was apparent in the group as a whole. As for the main analysis, we also performed t-tests comparing the difference between congruent and incongruent conditions for independent and interdependent primes for the naïve group. These tests revealed significantly larger difference scores for the interdependent word conditions (hard: 112 ms, soft: 57 ms) than the independent word conditions (hard: 61 ms, soft: 8 ms), for both execute hard and execute soft responses (hard: $t_3 = 2.684$, p = .038, soft: $t_3 = 2.132$, p = .05).

EMG Activity

To quantify the EMG activation for the APB muscle, the root mean square value of the raw signal on each trial was calculated using a time window of 300 ms. To select EMG bursts,

upon completion of the experiment, an experimenter manually identified onsets and offsets of the EMG burst underlying the response. A second individual who was not part of the experimental team independently selected onsets and offsets of EMG bursts for a sample participant and the inter-rater reliability was found to be high for both onsets (r=0.991, p<.001) and offsets (r=0.844, p<.001). We chose to use RMS EMG because it gives a measure of the total power in the EMG signal and also because it would allow effective comparison with previous studies from our laboratory (e.g., Obhi & Hogeveen, 2010). There was a significant main effect of cue type and video type on APB EMG activation ($F_{1,11} = 14.528$, p = .003 and $F_{1,11} = 10.886$, p = .007respectively). There was also a significant cue type x video type interaction ($F_{1,11} = 12.562$, p =.005). A paired-samples t-test showed that participants displayed more EMG activity when the cue instructed a hard squeeze and the video showed a hard squeeze (congruent condition, hard: 0.062 mVs) than when the cue instructed a hard squeeze and the video showed a soft squeeze (incongruent condition, hard: 0.053 mVs, $t_{11} = 3.555$, p < .003). Another paired-samples t-test showed that participants displayed more EMG activity in the APB when the cue instructed a soft squeeze and the video showed a hard squeeze (incongruent condition, soft: 0.021 mVs) than when the cue instructed a soft squeeze and the video depicted a soft squeeze (congruent condition, soft: 0.017 mVs, $t_{11} = 2.785$, p = .009). These results replicate the findings from our previous study, showing that EMG activity in the APB muscle was influenced in the direction of the incongruence between the video and the instructional cue (Figure 4).

There was also a significant cue type x video type x prime type interaction ($F_{1,11} = 5.655$, p = .037). A paired-samples t-test showed that when a colour cue instructing a hard squeeze was also an interdependent prime and the video showed a hard squeeze (interdependent congruent condition, hard: 0.065 mVs), participants showed more muscle activation than when the video

showed a soft squeeze (interdependent incongruent condition, hard: 0.049 mVs, t_{11} = 3.487, p = .003). In addition, APB EMG activity on trials when a colour cue instructed a soft squeeze and was also an interdependent prime and the video showed a hard squeeze (interdependent incongruent condition, soft: 0.023 mVs) was significantly larger than when the video showed a soft squeeze (interdependent congruent condition, soft: 0.017 mVs, t_{11} = 2.78, p = .009). Two more paired-samples t-tests compared the independent congruent and independent incongruent conditions. A significant difference was found between the independent incongruent soft condition (0.019 mVs) and the independent congruent soft condition (0.017 mVs, t_{11} = 1.838, p = .047), however, no significant difference was found between the independent congruent hard condition and the independent incongruent hard condition (p > .05).

To further investigate the different impact of the interdependent and independent primes on congruence effects we calculated the difference between congruent and incongruent conditions for each prime type. Paired-samples t-tests showed that the difference between congruent and incongruent conditions was greater for interdependent primes than for independent primes (interdependent incongruent minus congruent, hard: 0.017 mVs vs independent: 0.002 mVs, $t_{11} = 2.897$, p = .008; interdependent incongruent minus congruent, soft: 0.006 mVs vs independent: 0.002 mVs, $t_{11} = 2.031$, p = .034 - Figure 5).

An additional analysis for the group of participants who reported no awareness for any changes in the nature of the observed actions across trials was also performed. As can be seen in table 3, these participants showed the same pattern of results for EMG activity as the whole group. As for the main analysis, we also compared the differences between congruent and incongruent conditions for interdependent primes and independent primes. These tests revealed a significantly larger difference score for interdependent primes (0.014 mVs) than independent

primes for the hard cue condition (hard: 61 ms, $t_3 = 2.583$, p = .04). However, the difference score in the soft cue condition did not vary significantly as a function of word type (p > .05).

Discussion

The facilitation of RT for congruent videos and colour cues and the slowing of RT for incongruent videos and colour cues, along with the modulated level of EMG activity in the primary muscle replicate the findings from our previous study (Obhi & Hogeveen, 2010). The RT results support the assertion that our paradigm is an effective method of probing the motor resonance system. Specifically, if an observed action activates a motor representation that is incongruent with the cued response, then participants should be slower to respond due to interference between the competing motor representations. To complement the mental chronometry evidence, EMG activity displayed a significant modulation such that an observed hard squeeze movement elicits greater muscle activity in an instructed response and soft movements elicit less muscle activity in an instructed response. We conclude that motor resonance system activates a motor representation that is strictly congruent with the intensity of the observed movement. Hence, both the RT and EMG data illustrate co-activation of motor representations in the incongruent condition, versus activation of a single motor representation in the congruent condition.

Crucially to the present hypothesis, the effect of compatibility between observed and executed movements varied as a function of word type. A test of the congruent-incongruent effect sizes comparing the interSC and indSC primes showed that the motor priming effects were specifically enhanced by the interdependent self-construal words – both in terms of RT (<u>Figure</u>

3) and APB activity (<u>Figure 5</u>). Hence, our results suggest that the motor resonance system is specific to the intensity of muscle activation underlying an observed movement, and that this effect is sensitized by the priming of interdependent self-construal.

In Chartrand and Bargh's (1999) study, along with the behavioural mimicry literature en masse, participants report a lack of awareness of the target behaviours. In other words, if a participant observes a confederate playing with his pen and imitates this behaviour, the participant will typically report a lack of knowledge of the pen playing by the confederate or his or her own imitation. Mimicry, then, is automatic and unintentional. As a result, it is of interest whether or not the effects in the present study were automatic or due to the result of explicit cognitive strategies. During debriefing for the present study, four of the participants stated that they had failed to notice the varying intensities of the observed squeezing movement, referred to here as the 'naïve' group. Analyses of the naïve group revealed that the motor priming effect was still present in this condensed dataset. Despite the fact that the naïve group of participants were incognizant to the fact that the observed movement was changing, when that movement did not match their to-be-executed response they were slower to respond and the intensity of muscle activation underlying their squeeze was modulated in the direction of the incongruence. This suggests that the effect of an observed action on action execution was automatic and unintentional, since participants who failed to notice the changing nature of the observed movement were still affected by it.

Experiment Two

Introduction

In experiment two, we attempted to replicate the findings from experiment one using a direct measure of motor resonance (TMS induced MEPs), and investigated the correlation between mimicry and motor resonance. With regard to the former, we showed participants the same self-construal priming action stimuli from experiment one while inducing MEPs in the primary muscle in the observed action - APB. Our action stimuli in experiment two also included a neutral, action alone condition in order to determine whether interSC prime words increase motor resonance, indSC prime words decrease motor resonance, or both. Regarding the mimicry and motor resonance relationship, we added a dyadic interaction similar to those seen in the social psychological literature (Chartrand & Bargh, 1999) and correlated amount of mimicry to the facilitative effect of observed actions on motor corticospinal excitation. Our hypotheses from this study were two-fold: interSC prime words should enhance motor resonance during action observation, and, mimicry and motor facilitation should display a strong positive correlation. If interSC or indSC activation, known moderators of NCM, also moderate motor corticospinal excitation during action observation, and if a strong positive correlation is found, it would lend support to the assertion that motor resonance underlies NCM (although, again, this correlational link does not prove causation beyond doubt).

Methods

Participants

10 participants (5 male, 5 female, between the ages of 18 and 39) took part in the experiment for monetary compensation. All participants had normal or corrected-to-normal

vision and all were right-handed. The experiment conformed to local ethical guidelines and informed consent was obtained from all participants.

Apparatus and Stimuli

For the mimicry session, twelve photographs were chosen from various magazines (i.e. *The Economist: The world in 2010*) and websites (i.e. http://www.boston.com/bigpicture). The photos were cut out and mounted on black card stock. The same six photographs were always given to the confederate and the remaining six were always given to the participant.

The TMS experiment was programmed using Superlab v.4 (Cedrus Corporation, San Pedro, California) and run on a Dell desktop computer with stimuli displayed on a 20" LCD monitor. TMS was carried out with a Magstim Rapid² system (The Magstim Company ltd., Wales, UK). EMG data was recorded using a Biopac psychophysiological recording system (Biopac Systems Inc, Goleta, California). Digital pulses were sent from the computer running Superlab to the Biopac system, which in turn was used to trigger TMS pulses through a solid state relay drive. Motor-evoked potentials (MEPs) were measured with pairs of 8-mm surface electrodes placed in a belly-tendon arrangement over the APB muscle of the participant's right hand. A ground was placed on the ulnar styloid of the right wrist. The EMG signal was acquired with a 1KHz sampling rate, amplified (to 5.0 mV) and filtered (band pass 10-500Hz), and sent to a laptop computer for offline analysis.

Experimental stimuli were videos depicting a right hand (palm facing down) squeezing a rubber ball between the thumb and index finger hard, such that the rubber ball was substantially deformed (Figure 6). The videos consisted of a single squeeze repeated five, six, seven, eight or nine times. Self-construal primes were superimposed in black font throughout some of the

videos. A list of 30 self-construal primes (15 independent, 15 interdependent) was adapted with permission from Kühnen and Hannover (2000), the same source used by van Baaren et al. (2003). A complete list of the words used in experiment two is given in <u>Table 4</u>. Video-editing was performed using Final Cut Express v.4 (Apple Corporation, Cupertino, California).

Design and Procedure

Non-conscious mimicry procedures

Each experimental session began with a 5-10 minute dyadic interaction between the participants and a confederate, which took place under the guise of a photo description task, akin to previous NCM literature (i.e. Chartrand & Bargh, 1999). Initially, the participant was seated in a chair that was at a 45° angle to the experimenter, and told to wait for a few minutes while the experimenter went to get the second 'participant'. This time period, approximately 2 minutes per participant, served as the baseline phase. After entering the room, the confederate was seated in a chair 1.2 meters from the participant, at 45° to the participant and the experimenter. During each dyadic interaction, the confederate shook her foot approximately once every five seconds. The experimenter was seated behind a desk, draped with black fabric to occlude vision of his lower half. With this arrangement, participants could see the confederate's, but not the experimenter's, feet during the interaction. A video camera was covered with a black sheet and placed in the laboratory to covertly record each participant for offline analysis by two coders who were not involved in the experiment.

After the dyadic interaction, the confederate was told that they had completed their portion of the experiment, and the participant was asked a series of questions once the confederate departed. The questions included: i) did you think the other 'participant' might have

anything to do with the experiment, and ii) did the other 'participant' display any particular gestures, postures, mannerisms or ways of speaking that you noticed. After the dyad and interim debrief, participants moved on to the TMS portion of the experiment, which they were told was part of a separate and unrelated experiment.

TMS procedures

Participants were seated with their right arms flexed at 90° and resting on a pillow positioned on the desk immediately in front of the monitor, and a cardboard box and black fabric were used to occlude vision of their hand. The experimenter located the vertex using the inionnasion line and the preauricular points at the posterior end of each zygomatic arch as landmarks. TMS was delivered through a figure-eight coil, held normal to the scalp and 45° to midline, with current flowing in a posterior-anterior direction over the left primary motor cortex. Stimulation began at 70% stimulator output at the point midway between the left preauricular point and vertex and gradually moved in a ventral-dorsal direction until the site eliciting the greatest MEP in the right APB muscle was identified. The optimal location was marked on a lycra swim cap worn by participants, and a mechanical arm was used to hold the coil in a fixed position (Figure 7). Once the coil was in position, stimulator output was decreased at 5% intervals to determine resting motor threshold, defined as the lowest intensity sufficient to elicit five MEPs of approximately 1 mV amplitude out of 10 TMS pulses delivered three seconds apart. For the sample of participants in experiment two, stimulation intensity ranged from 56% to 70% (mean: 64.1%) of stimulator output. During the baseline and experimental trials, the stimulator was set to 10% above resting motor threshold.

Prior to video presentation, baseline corticospinal excitation was assessed by delivering 30 TMS pulses at 5 second intervals while participants passively viewed a fixation stimulus. After the baseline block, each participant was exposed to three randomized blocks of 75 trials showing a rubber ball being squeezed. Specifically blocks were comprised of: 25 neutral (no self-construal prime), 25 interdependent and 25 independent trials. Each block contained 30 TMS pulses, which were delivered at points of maximum flexion during the action alone (10), intSC (10) and indSC (10) videos. Participants were instructed to count the number of squeezes contained in each video and report the number verbally at the end of each trial, to ensure attention to the action.

Following the TMS session, participants were asked one more question: did you notice anything about the types of words being presented in this part of the experiment? After responding, the hypotheses, purpose and methods of the study were elucidated.

Results

Video Coding & Inter-rater Reliability

Two independent judges who were not involved in the experiment coded videos. Two time periods were analyzed for each participant: the number seconds before the dyad began (baseline phase) and the number of seconds spent interacting with the confederate (interaction phase). The video coders identified the total number of seconds participants shook their foot whilst seated during both the baseline and interaction phases. Ratios were calculated to determine the amount of time spent foot shaking with respect to the total amount of time per condition (i.e. baseline foot shaking / baseline phase; interaction foot shaking / interaction

phase), which were then used to determine an overall mimicry ratio (\mathbf{M} = interaction ratio / baseline ratio). When participants showed nil seconds of foot shaking in either the baseline or interaction conditions, 1 was added to both constituents of the \mathbf{M} ratio. The inter-rater reliability measures were significant for both the baseline (r = .761, p = .0055) and interaction (r = .555, p = .048) phases of the dyadic scenario.

Outliers

MEP amplitudes were defined as the maximum peak to peak (P-P) value in a given trial. However, if the maximum P-P detection fell outside of a 15-40 ms epoch after delivery of TMS, it was considered spontaneous (i.e., non-specific) EMG activity, and those trials were discarded. In addition, when MEPs were greater than or less than three standard deviations from the mean, trials were omitted from overall analysis. In total, this procedure resulted in the removal of 5.00% of the data.

Motor Resonance

In order to confirm that our video stimulus does indeed activate the observer's corticospinal system, the first statistical analyses were one-tailed t-tests ensuring significant MEP increases in the action alone, intSC and indSC conditions, compared to baseline. Mean MEP amplitudes were significantly higher than baseline (baseline: .74 mV) in the action alone and intSC conditions (action alone: 1.09 mV, $t_9 = 3.79$, p = .002; intSC: 1.25 mV, $t_9 = 4.119$, p = .0015). However, mean MEP amplitudes in the indSC displayed an increase from baseline that did not quite reach significance (indSC: .96 mV, $t_9 = 1.605$, p = .0715; Figure 8).

Motor Resonance and Self-Construal Activation

In order to determine whether self-construal priming had a significant effect on motor resonance during action observation, mean MEP amplitudes for each condition were entered into an ANOVA with one within-subjects factor (condition: action alone, intSC or indSC). There was a significant main effect of condition in the ANOVA ($F_{3,27} = 9.474$, p < .001). Mauchly's test showed that the assumption of sphericity in the ANOVA was violated, which was adjusted using the Greenhouse-Geisser correction ($F_{1.81,16.29} = 9.474$, p = .002). Planned contrasts were used to test for significant mean MEP differences between conditions. These contrasts showed that mean MEP amplitude was significantly larger in the intSC than the action alone condition ($t_9 = 2.591$, p = .0145). Mean MEP amplitudes in the action alone condition were larger than the indSC condition, but the difference was not quite significant ($t_9 = 1.594$, p = .0725). Most important for the present hypothesis was the contrast between mean MEP amplitudes in the two self-construal prime conditions, which showed a significantly higher mean for the intSC than the indSC prime words ($t_9 = 3.726$, p = .0025).

Although the mean MEP analyses confirmed our hypothesis regarding self-construal priming and motor resonance, this process did not control for individual differences in baseline corticospinal activity, which was significant (p < .001). In order to control for individual differences in tonic activity, mean MEP amplitude in each condition was divided by mean MEP amplitude in the baseline phase, providing a 'motor facilitation ratio'. The ratios were then compared in a series of one-tailed t-tests. Motor facilitation ratios in the intSC condition were significantly larger than the action alone condition (intSC: 1.95 vs action alone: 1.67, $t_9 = 2.87$, p = .009), and were also significantly larger than in the indSC condition (intSC vs. indSC: 1.53, t_9

= 4.391, p = .001; <u>Figure 9</u>). However, the difference between motor facilitation in the action alone and indSC conditions did not reach significance (action alone vs. indSC, p = .1).

Motor Resonance and Nonconscious Mimicry

To investigate the relationship between NCM and motor resonance, a Pearson correlation coefficient was calculated between i) \mathbf{M} and ii) MEP amplitude increase in the action alone condition. There was a large range in the amount of mimicry displayed by participants, with the lowest mimicker's \mathbf{M} value at 0.01, and the highest mimicker at 3.08 (mean: 0.94). Since we were testing the theory that motor resonance underlies mimicry, we *a priori* predicted that any bivariate correlation between levels of mimicry and levels of motor resonance would be positive. In view of this prediction, we report the correlation along with a one-tailed p value. Specifically, the correlation between levels of mimicry and levels of motor resonance was moderately positive (r = .551), and was significant (p = .0495; Figure 10).

Discussion

The finding that motor corticospinal excitation during action observation was significantly higher in the intSC than the indSC condition strengthens our conclusion from experiment one, namely, that intSC priming induces hyper motor resonance. Also of interest, the action alone condition induced motor facilitation to a lesser extent than the intSC condition, whereas indSC priming action videos did not result in significant motor facilitation. Collectively, these results seem to indicate that motor resonance was elicited by our action videos (aa/b), and this effect was significantly increased by the presence of intSC primes (intSC/b), and slightly decreased by indSC primes (indSC/b).

Based on the theory that mimicry is initiated by a human mirror system, we hypothesized a strong positive correlation between mimicry and motor resonance. However, our results displayed only a moderate positive correlation between these variables. The results from the mimicry dyad itself were also unexpected. In our mimicry dyad, over half of the participants (6/10) displayed a reduction in foot shaking during the interaction. This result is surprising given the robust mimicry reported in the social psychology literature. There are three possible explanations for this discrepancy. First, Chartrand and Bargh's (1999) study tested 39 participants, in contrast to the 10 used in experiment two. It is possible that our sample was simply not large enough to provide an apt representation of the population, instead including a small group of low mimickers. Second, it is possible that our chosen target behaviour was the reason for our failure to consistently display mimicry. Foot shaking was chosen in order to replicate one of the behaviours used in Chartrand and Bargh (1999), but, in retrospect, another option such as face rubbing might provide a more salient target behaviour. Lastly, there are a number of conditions in which the desire to affiliate is not present and mimicry is reduced (i.e. Johnston et al., 2002; Yabar et al., 2006; Karremans & Verwijmeren, 2008). Thus, it is probable that a number of social, cognitive, affective, motivational and attitudinal factors, such as the nature of an individual's self-construal, were moderating mimicry during our dyadic interaction. The fact that moderators beyond basic action observation influenced our mimicry results does not preclude the assertion that the motor resonance system underlies NCM. To be clear, in our action observation task, there was very little social psychological information portrayed, other than the fact that the hand performing the action was white and female. In contrast, any dyadic interaction in real life (such as in our mimicry session) contains myriad social cues. Thus, the

fact that a strong positive correlation was not found could be explained by this basic difference in the two stimulus displays.

This line of reasoning generates a prediction for future work: action observation tasks in which rich social information is provided should produce motor resonance that is highly correlated with levels of mimicry, compared to action observation tasks providing very little social information. Hence, it is very possible, in fact likely, that the various moderating variables influence emotional brain activity in the limbic system, or arousal signals travelling from the brain stem. For example, observing and imitating emotional facial expressions modulates activity in the motor resonance system through a limbic-insular network (Carr et al., 2003). There is also recent evidence that heightened emotional arousal is associated with an increase in motor corticospinal excitability (Coombes et al., 2009). Despite the connection we have drawn using a self-construal manipulation, further investigation will be needed to strengthen the assertion that the variables that moderate NCM do so by moderating motor resonance.

GENERAL DISCUSSION

There is a broad literature on the form and function of NCM in social interactions (Chartrand & van Baaren, 2009), and an equally extensive catalogue of research concerning the human mirror system (Rizzolatti & Sinigaglia, 2008; Iacoboni, 2009). However, until very recently (i.e. Spengler et al., 2010a;b; Hogeveen & Obhi, in press), there has been a complete lack of research investigating whether the mechanisms underlying mimicry are the same as those involved in action observation. This is likely due to the fact that, typically, mimicry and action observation studies have been carried out by different groups of researchers. The work presented in this thesis helps to close that divide by showing that a moderator of NCM also affects the

motor resonance system, and by using established techniques from social psychology (mimicry dyad, Chartrand & Bargh, 1999) and cognitive neuroscience (MEPs, Fadiga et al., 1995) on the same population.

In experiment one, we showed that a known moderator of mimicry also modulates performance on a motor priming task. Motor priming is an indirect manifestation of motor resonance – the increased activation in movement specific motor representations during action observation. Due to the finding that interSC priming increases mimicry (van Baaren et al., 2003) and under the assumption that the motor resonance system underlies NCM, we specifically predicted that interdependent primes would sensitize motor resonance, which, in turn, would increase motor priming effects. Our results confirmed this prediction, with a robust effect size present when interSC was activated, and a marginal effect present when indSC was activated. We interpret this finding as a confirmation of our prediction: that the activation of interSC results in an increase in the movement specific sensitivity of the neural systems that respond to observed action, or *hyper motor resonance*.

Our assertion of interSC-induced hyper motor resonance is not the only possible interpretation of our findings from experiment one. A recent study by Spengler et al. (2010a) employed a motor priming paradigm and showed a decreased influence of an observed movement on responses when participants watched themselves perform the task in a mirror. The mirror paradigm is a method of inducing heightened self-focus (Duval & Wicklund,1972). In light of this evidence, in experiment one it is possible that the indSC primes were reducing the degree of motor mimicry by activating self-focus, which reinforces current internally produced action intentions (Spengler et al., 2010a). If this is the case, then our interSC primes may not be inducing hyper motor resonance so much as representing a baseline from which indSC-induces

hypo motor resonance. In experiment two, an action alone condition with no self-construal prime word was included in order to determine the direction of the effect.

In experiment two, participants passively observed the same self-construal action stimuli from experiment one with an added neutral, or action alone, condition. Participants watched the videos while TMS pulses were delivered over left M1 and MEPs were recorded from their relaxed right APB muscle. Regarding our intSC-induced hyper motor resonance hypothesis, MEP amplitudes were significantly higher during the presentation of intSC videos than the action alone condition. With respect to a possible indSC-induced hypo motor resonance, MEP amplitudes were reduced in the indSC compared to the action alone condition, however this difference did not reach significance. The significant hyper motor resonance caused by intSC primes, and nearly significant hypo motor resonance effect of indSC primes, parallels the effect of self-construal priming on mimicry (van Baaren et al., 2003), and provides support to the suggestion that the mirror system may play an important role in NCM (Iacoboni, 2009).

An interesting question for future research would be to look at the network of brain areas involved in self-construal priming. Although experiments one and two nicely display a facilitation of motor resonance when interSC is activated, and a reduction when indSC is activated, they fail to demonstrate the pattern of neural connectivity that allows self-construal priming to affect motor resonance. A recent study showed that priming independent or interdependent self-construal (or individualism or collectivism) reliably modulates hemodynamic activity in the dorsal medial prefrontal cortex (dMPFC) (Harada et al., 2010). In the future it would be interesting to determine whether stronger effective connectivity exists between dMPFC and the purported human mirror areas, such as IFG, while the interdependent self is primed. In addition to this possible neurobiological extension, it would be interesting to explore whether

variables of the model are capable of modulating the observer's self-construal without the use of priming techniques. For example, if the disembodied limb in the present study were replaced by a whole-body model displaying the squeeze movements, and one of those models was a fellow university student whereas another model was a person wearing prison attire, it may be predicted that interdependent construal would be activated while viewing the former, in contrast to the latter, model.

Our self-construal manipulation fails to answer a key question: to what extent are the mechanisms underlying action observation able to account for mimicry? In order to answer this question, we included a mimicry dyad similar to those used in the social psychological literature at the beginning of experiment two, and compared individual differences in NCM to individual differences in motor facilitation during action observation. It was hypothesized that if motor resonance underlies mimicry, a strong positive correlation should exist between MEP facilitation and NCM. We report a very modest correlation between mimicry and motor resonance. Hence, our hypothesis was not fully supported, and the results seem to indicate that motor resonance, in the absence of social information is not enough to elicit mimicry on its own. Rather, in line with the social psychological literature on NCM, it would appear that a host of social, cognitive, affective, motivational and attitudinal factors interact with the motor resonance system to produce mimicry (Figure 11). We must also concede that, although we measured motor resonance indirectly and directly, the experiments in this thesis are unable to confirm whether a human mirror system per se, mediates NCM. Future work with fMRI will be required to establish the functional connection between such a system and NCM.

In sum, through the use of a self-construal manipulation, the present research illustrates, for the first time empirically, a relationship between mimicry and motor resonance. Again, this

relationship has been suggested many times in the literature, but has not been verified experimentally. Our work is the first step in gaining a full understanding of the neural mechanisms underlying NCM. The failure to find a strong positive correlation between motor resonance and NCM suggests that consideration of the moderating effects of a host of social variables on motor resonance is required in future work. Indeed, in general, a more dynamic and intricate analysis of the 'social brain' is required to form a comprehensive neurobiological understanding of *why* we are social chameleons.

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Figure Captions

<u>Figure 1:</u> Sample stimuli of each condition from experiment one. The independent incongruent soft condition (in red) consisted of an independent prime cueing a soft response while observing a hard squeeze video. The interdependent incongruent hard condition (in blue) consisted of an interdependent prime cueing a hard response while observing a soft squeeze video. Each experimental condition (8) occurred 20 times (once per word) in the short cue onset video and 20 times (once per word) in the long cue onset video.

<u>Figure 2:</u> RT two-way interaction (Cue x Video). Mean RT for the congruent (dashed line) versus incongruent (continuous line) conditions. Error bars represent the standard deviation of each data series.

<u>Figure 3:</u> RT RT difference scores. Bars represent the mean difference between congruent and incongruent conditions for the interSC (black) and indSC (grey) word types. Error bars represent the standard deviation of each data series.

<u>Figure 4:</u> APB EMG activity, main effect of video type. Mean APB EMG activity for the hard video (continuous line) versus soft video (dashed line) conditions. Error bars represent the standard deviation of each data series.

<u>Figure 5:</u> APB EMG difference scores. Bars represent the mean difference between muscle activity during soft videos and hard videos for the interSC (black) and indSC (grey) word types. Error bars represent the standard deviation of each data series.

<u>Figure 6:</u> Sample stimuli of each condition from experiment two. Each experimental condition (3) was paired with a TMS pulse 30 times (twice per word).

Figure 7: Depicts the experimental apparatus as they were set-up during experiment two.

<u>Figure 8:</u> Grand average MEPs by condition from experiment two. The epoch at 15-40ms following TMS delivery was extracted and sorted by condition, and those waveforms were averaged. Asterisks indicate significant motor facilitation, or increase from the baseline phase.

<u>Figure 9:</u> Motor facilitation ratios by self-construal prime type from experiment two. Mean MEP amplitudes for the indSC and interSC conditions were divided by baseline to form the ratio.

<u>Figure 10:</u> Scatterplot of the relationship between motor resonance (average MEPs in action alone condition divided by baseline, aa/b) and mimicry (interaction foot shaking divided by baseline, **M**) from experiment two.

<u>Figure 11:</u> Theoretical model of the relationship between mimicry and motor resonance based on the literature summarized by Chartrand & van Baaren (2009) and work presented in this thesis, yellow line indicates potential future work and red lines indicate established connections.

Table Captions

- <u>Table 1.</u> InterSC and indSC prime words used in experiment one.
- Table 2. Mean RTs (ms) for the naïve and overall datasets from experiment one.
- Table 3. Mean APB EMG activity (mVs) for the naïve and overall datasets from experiment one.
- Table 4. InterSC and indSC prime words used in experiment two.

Figure 1.

		Video Type						
		На	Hard		Soft			
		Independent	Interdependent	Independent	Interdependent			
Туре	Hard	done	st HL atfo. J	sion	atisticati v			
Cue	Soft	. Prese	रकर [्] ⁄‰ இ.?	≈® % €	CEN, STEX			

Figure 2.

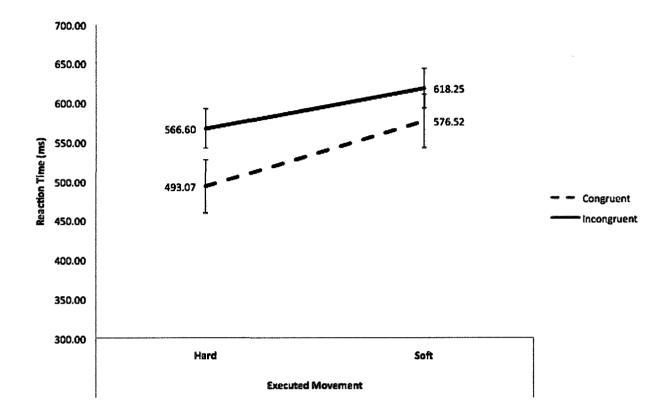


Figure 3.

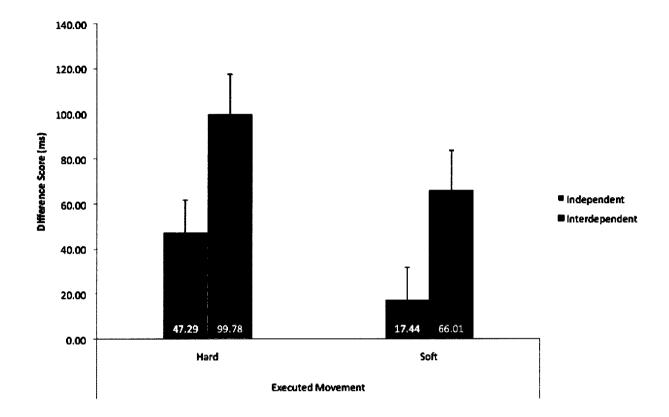


Figure 4.

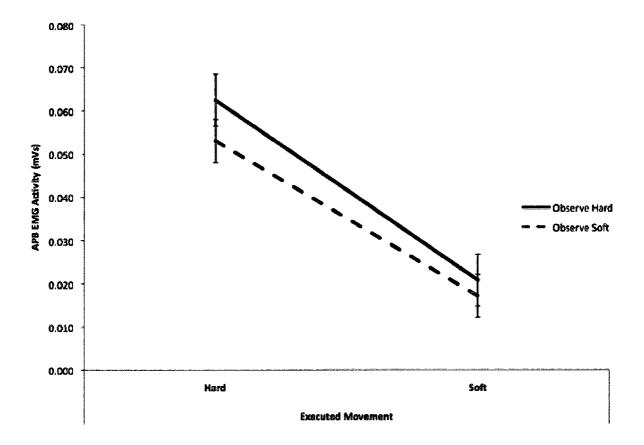


Figure 5.

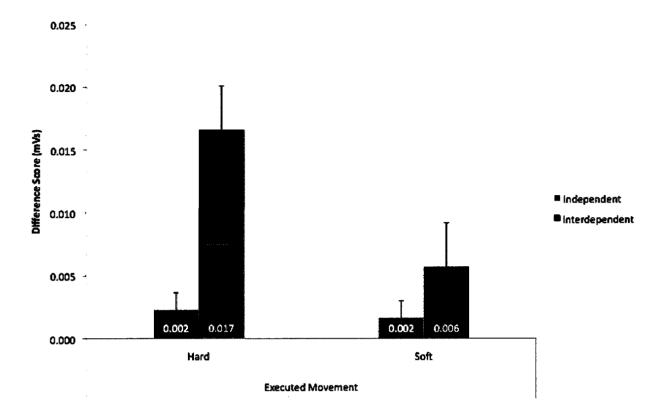


Figure 6.

INDEPENDENT	ACTION ALONE	INTERDEPENDENT
UNIQUE		HELP
*	:	
1		

Figure 7.



Figure 8

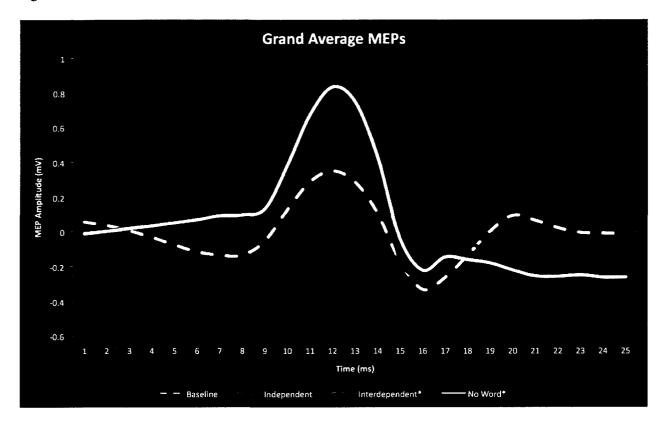


Figure 9.

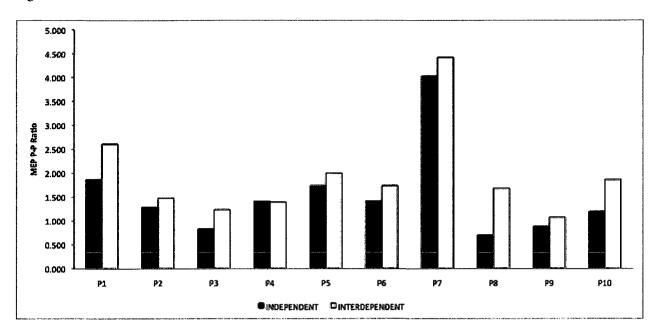


Figure 10.

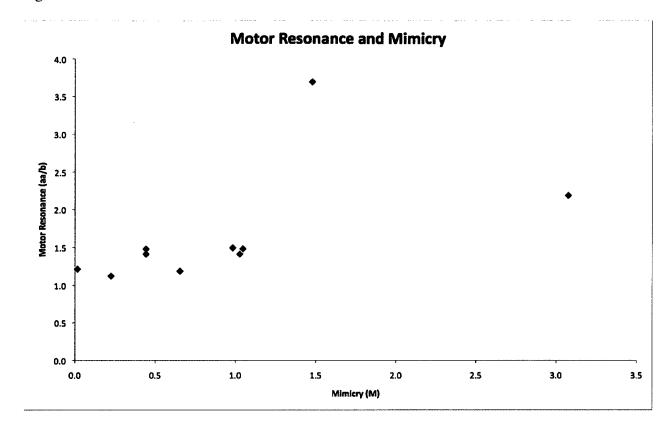
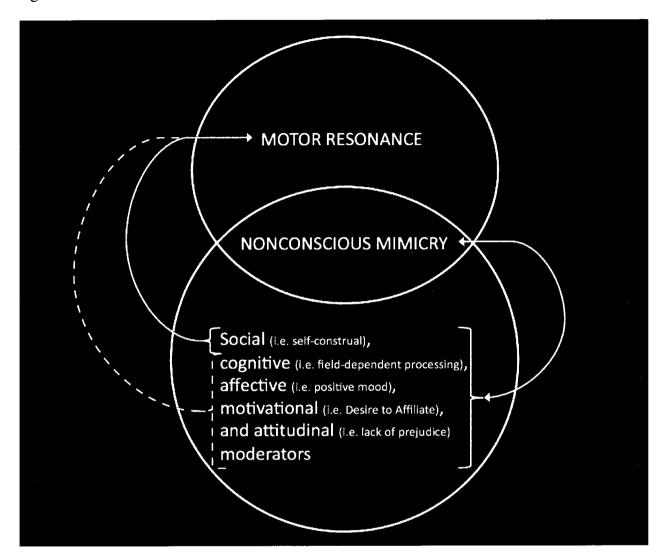


Figure 11.



Tables

Table 1.

IndSC	InterSC		
Independent	Together		
Individuality	Integrate		
Unique	Help		
Autonomous	Others		
Distinct	Family		
Life	Social		
Distinguished	Give		
Myself	Lives		
Singular	Team		
Unconnected	Connected		
Apart	Accommodate		
Solo	Friend		
Lone	Group		
Oneself	Cooperate		
Alone	Companion		
Special	Relationship		
Mine	Affiliation		
Solitary	Community		
Differ	Dependence		
Self	Alliance		

Table 2.

	Hard Cue				Soft Cue			
	Hard Video		Soft Video		Hard Video		Soft Video	
	indSC	interSC	indSC	interSC	indSC	interSC	indSC	interSC
Naïve Group	465.75	451.25	526.77	563.72	570.94	597.68	562.94	540.67
Overall								
Group	500.29	485.85	547.58	585.63	602.23	634.27	584.78	568.26

Table 3.

Hard Cue Soft Cue Soft Video Hard Video Hard Video Soft Video indSCinterSC indSCi<u>nterSC</u> indSCinterSC indSC interSC Naïve Group 0.050 0.012 0.046 0.044 0.036 0.015 0.016 0.013 Overall Group 0.060 0.065 0.057 0.049 0.019 0.023 0.017 0.017

Table 4.

IndSC	InterSC
Independent	Together
Individuality	Integrate
Unique	Help
Autonomous	Others
Distinct	Family
Distinguished	Social
Myself	Common
Apart	Accommodate
Oneself	Cooperate
Lone	Relationship
Singular	Team
Unconnected	Friend
Solo	Companion
Mine	Affiliation
Solitary	Dependence