



# HHS Public Access

Author manuscript

*Neuropsychologia*. Author manuscript; available in PMC 2016 December 01.

Published in final edited form as:

*Neuropsychologia*. 2015 December ; 79(0 0): 233–245. doi:10.1016/j.neuropsychologia.2015.04.005.

## Common Coding and Dynamic Interactions Between Observed, Imagined, and Experienced Motor and Somatosensory Activity

Laura K Case, PhD<sup>1,2</sup>, Jaime Pineda, PhD<sup>3</sup>, and Vilayanur S Ramachandran, PhD<sup>1</sup>

<sup>1</sup> Center for Brain and Cognition, University of California, San Diego

<sup>2</sup> Pain and Integrative Neuroscience Branch, National Center for Complementary and Integrative Health, National Institutes of Health, Bethesda, MD

<sup>3</sup> Department of Cognitive Science, University of California, San Diego

### Abstract

Motor imagery and perception- considered generally as forms of motor simulation- share overlapping neural representations with motor production. While much research has focused on the extent of this “common coding,” less attention has been paid to how these overlapping representations interact. How do imagined, observed, or produced actions influence one another, and how do we maintain control over our perception and behavior? In the first part of this review we describe interactions between motor production and motor simulation, and explore apparent regulatory mechanisms that balance these processes. Next, we consider the somatosensory system. Numerous studies now support a “sensory mirror system” comprised of neural representations activated by either afferent sensation or vicarious sensation. In the second part of this review we summarize evidence for shared representations of sensation and sensory simulation (including imagery and observed sensation), and suggest that similar interactions and regulation of simulation occur in the somatosensory domain as in the motor domain. We suggest that both motor and somatosensory simulations are flexibly regulated to support simulations congruent with our sensorimotor experience and goals and suppress or separate the influence of those that are not. These regulatory mechanisms are frequently revealed by cases of brain injury but can also be employed to facilitate sensorimotor rehabilitation.

### Keywords

Simulation; Mirror neuron system; Sensory referral; Motor referral; Somatosensation; Imagery

---

Corresponding author: Laura K Case, National Center for Complementary and Integrative Health, National Institutes of Health, Bethesda, Maryland, [laura.case@nih.gov](mailto:laura.case@nih.gov), phone +1-301-435-1720, fax 301-480-5678, Current mailing address: BG 10-CRC RM 4-1730 Mail Stop 1302, 10 Center Dr, Bethesda, MD 20892.

**Publisher's Disclaimer:** This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final citable form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

## Introduction

In the nearly two decades since the discovery of mirror neurons in monkeys (Gallese et al 1996), much research has explored the extent of “common coding” between action and action perception. Further research has explored the degree to which mirror neurons- or at least “mirror mechanisms”- are necessary or sufficient for higher-level abilities like action comprehension, mentalizing, and empathy (e.g. Sinigaglia 2013; Iacoboni 2009). Other implications of these shared representations, however, have received less attention. Schütz-Bosbach & Prinz (2007) astutely point out that in addition to motor resonance- the influence of perceived action on the motor system (e.g. Rizzolatti et al., 2001)- common coding also implies perceptual resonance- an influence of action on action perception. In other words, by virtue of overlapping neural representation, activation of motor representations by “real” motor production and “simulated” motor activity exert mutual influence on each other. This overlap between observed, imagined, and produced movements raises the question of how we maintain control over our perception and behavior. In the first half of this paper we review interactions between motor production, observed movement, and imagined movement, and explore how their interaction is regulated.

The motor system, of course, is not the only system that contends with vicarious and imagined representations. Arguably each sensory domain must carefully regulate the influence of imagined sensations, observed sensations, and other forms of vicarious sensation. The somatosensory system, however, works in especially close consort with the motor system, and several authors have argued for the existence of a somatosensory mirror system (e.g. Bradshaw & Mattingley 2001; Fitzgibbon et al 2012) containing overlapping representations of sensation, observed sensation, and somatosensory imagery. We thus constrain our current discussion to the motor and somatosensory domains. As in the motor system, overlapping neural representations in the somatosensory system imply mutual interaction between afferent sensation and vicarious or imagined sensation. In the second half of this paper we review evidence of such interactions and for their regulation.

Observed and imagined somatosensory and motor activity can be considered together as forms of simulation. Simulation is commonly invoked to describe a variety of cognitive processes from automatic motor resonance to conscious reasoning about the goals and intentions of others (for a discussion of varying theories of simulation in social cognition, see Decety & Grèzes 2006). In the current review, we do not utilize this term in order to endorse simulation accounts of action understanding (e.g., the idea that observed action automatically activates matching motor representations in the viewer that afford understanding of the observed action; Gallese & Goldman 1998). Simulation here is considered generally as an activation of neural representations of movements that are not produced overtly, or sensations that are not caused by external somatosensory stimulation (similar to Decety & Grèzes 2006). To the extent that observed and imagined movements and sensations activate representations shared with efferent movements and afferent sensations, we can consider them simulations of the corresponding “real” sensorimotor state they emulate. Regardless of whether these simulations are drawn upon by additional cognitive processes, these activations influence our perception and our actions.

We suggest that interactions between simulated and “real” sensorimotor processes occur in both the sensory and motor domains. In addition, we argue that numerous neural processes flexibly regulate the influence of simulation on action and perception. This flexible regulation supports simulations that are congruent with one's experiences and goals and suppresses or separates the influence of those that are not. In particular, we argue that simulation is regulated by sensorimotor feedback, frontal and transcallosal inhibitory processes, and calculations of self-identification and social affiliation. Throughout, we rely on cases of brain damage and deafferentation to explore the role of specific brain areas in regulation of simulation. Deafferentation removes motor capacity and motor feedback as well as afferent sensation, allowing us to see the role that sensorimotor feedback normally plays in simulation. Similarly, brain lesions allow for study of the role of a particular brain area in regulating simulation. Cases of brain damage to sensory and motor regions, however, also provide an opportunity to capitalize on shared representations and use simulated motor and sensory activity to support sensorimotor rehabilitation. These examples further demonstrate the dynamic interactions between simulated and “real” sensorimotor activity.

## 1. The Motor System

### Motor Referral

**Overlapping representations of action and action perception**—When we observe others move, we simulate their actions in our motor system (e.g. Jeannerod, 1994; Grèzes & Decety, 2001; Rizzolatti et al., 2001). We use the term ‘motor referral’ to describe this covert, spontaneous mirroring of others.<sup>1</sup> Behavioral, functional brain imaging, and transcranial magnetic stimulation (TMS) studies have accumulated evidence of brain areas with mirror properties in humans: areas active during both the performance and observation of a given action (e.g. Fadiga et al., 1995; Altschuler et al 1997; Cochin and colleagues 1999; Muthukumaraswamy and Singh, 2008; Keysers & Gazzola 2009; Ushioda et al., 2012). Individual subjects consistently activate shared voxels during functional magnetic resonance imaging (fMRI) of observed and performed movements (Keysers & Gazzola 2009). fMRI adaptation studies have obtained mixed results (e.g. Chong et al 2008 versus Lingnau et al 2009), but single-cell recordings in surgical patients have provided direct evidence of neurons that respond to both observation and execution of actions (Mukamel et al 2010). In addition, studies of primary motor cortex (M1) excitability during action observation show subthreshold activation of peripheral muscles involved in the observed movement (Fadiga et al 1995; Aziz-Zadeh et al 2002; Maeda et al 2002; Strafella and Paus 2000; Hari et al., 2014).

**Interactions Between Action and Action Perception**—An implication of common coding in the human mirror system is that movements we observe might influence movements we produce. Indeed, a number of studies evidence the influence of observed actions on produced actions. Similar action representations appear to facilitate one another. Observing finger movements, for example, increases force production of finger movements (Porro et al 2007). Participants are faster to perform finger movements congruent with those

---

<sup>1</sup>Motor referral can also occur in response to non-conspecifics for species-similar movements like biting; see Buccino et al (2004), and to movement of robots; see Oberman et al (2007a).

they observe (Brass et al 2001), and faster to perform a grasping action when shown a hand position similar to the target (Craighero et al 2002). Conversely, action production affects action perception, as Schütz-Bosbach & Prinz (2007) argue. Moving a body part facilitates recognition of that body part's position on another person (Reed & Farah 1995), and rotating a knob biases perceived apparent motion in the same direction (Wohlschläger 2000). Hand actions facilitate visual discrimination of congruent hand postures (Miall et al 2006).

Actions and observed actions that are dissimilar from one another, however, often exhibit interference effects. When an observed action is incongruent with motor planning it can slow down the motor response (e.g. Brass 2000), perturb the path of movement in space (Kilner et al 2003), or increase the observer's body-sway (Tia et al 2011). Similarly, movements can alter the perception of discrepant actions. Walking at a different speed than an observed model impairs the actor's estimation of the model's walking speed (Jacobs & Shiffrar, 2005), wearing ankle weights lowers an actor's estimate of how high an unencumbered person can jump (Ramenzoni et al, 2008), and biting a pencil or tongue depressor (to block simulation-related motor action in the mouth) interferes with recognition of happy faces (Oberman et al 2007b) and visual perception of speech (Turner et al 2014). Finally, preparing for a particular movement interferes with response time to imitate an incongruent movement- more so than an unrelated distracter (Obhi & Hogeveen 2013). Motor referral is also sensitive to timing. Even when asked to not synchronize with one another, two people performing rhythmic actions tend to entrain to each other's rhythm (Marsh et al, 2009). These studies suggest that motor referral and motor production facilitate or interfere with one another depending on the spatiotemporal and postural congruence of the observed and performed actions.

**Processes that Regulate Motor Referral**—The interactions between motor referral and motor production suggest that these processes may mutually depend on- and constrain- each other. Indeed, evidence from phantom limb patients suggests that motor activity normally inhibits motor referral. Amputees lack the ability to produce motor movements in their absent limb. Yet when their healthy arm is visually superimposed in a mirror onto their phantom arm, amputees frequently reports that the phantom arm feels like it is moving (Ramachandran & Hirstein 1998). This motor referral is exploited in mirror box therapy, an effective method of pain reduction for many patients with painful phantom limbs (Ramachandran et al 1995; Ramachandran & Rogers-Ramachandran 1996; Chan et al 2007). Mirror box therapy demonstrates that motor referral can occur in the absence of concurrent motor feedback. Indeed both healthy individuals and individuals with non-painful phantom limbs show activation of M1 and primary sensory cortex (S1) during mirror box motor referral (Diers et al 2010). The patients with non-painful phantom limbs actually showed *greater* activation of M1 than the control subjects did. This suggests that motor activity may normally inhibit simulation of observed actions.

On the other hand, reductions in motor production after botox injection suggest that motor feedback normally facilitates simulation. Reducing muscular feedback from the face with botox impairs perception of facial expression (Neal & Chartrand 2009) and reduces emotional response in the amygdala (Hennenlotter et al., 2009), while enhancing muscular feedback from the face enhances perception of facial affect (Neal & Chartrand 2009). This

suggests that motor feedback from the face normally enhances motor referral, improving emotional simulation. In line with this, individuals following instructions to suppress their own facial expressions are less sensitive to the facial affect of others, while mimicking others' expressions improves sensitivity to others' affect (Schneider et al 2013). Why do amputation and botox have different effects on motor referral? It may be that simulation is inhibited by default in the limbs- important for locomotion- but not in the face, where simulation can give more help than harm.

Motor referral may also be regulated by the frontal lobes. Since spontaneous, overt imitation of actions is uncommon, it has been suggested that the frontal lobes tonically inhibits imitation. Brass et al (2001) performed fMRI while subjects executed pre-instructed finger movements in response to an observed finger movement that was either congruent or incongruent with the performed movement. On incongruent trials, there was strong activation of the dorsolateral prefrontal cortex, right frontopolar cortex, right anterior parietal cortex, and precuneus, suggesting prefrontal involvement in response inhibition of imitative actions. Indeed, damage to the prefrontal lobes seems to disrupt frontal lobe suppression of mirror areas, causing Echopraxia, a condition in which patients indiscriminately imitate the movements they observe (Brass et al 2003; Brass et al 2005). Echopraxia can also arise as a result of basal ganglia dysfunction or injury (Rizzolatti et al 2009), implicating cortico-limbic circuitry in the regulation of motor activity. In addition, automatic mirroring can be suppressed by attention, context, and task goals (for a summary, see Cross & Iacoboni 2014).

Brass et al (2005) also found that suppression of an imitative response involved the right temporo-parietal junction. The right inferior parietal cortex is involved in distinguishing imitating from being imitated (Decety et al, 2002), and the right temporo-parietal junction plays a role in perspective taking and judgments of self-agency (Brass & Heyes, 2005). The involvement of these brain areas suggests that judgments of self and other may contribute to regulation of the influence of observed actions on action production. This idea is supported by work showing diminished sensorimotor referral to observation of pain in racial out-group members (Avenanti et al, 2010). Referral was not diminished to unfamiliar "out-group" violet-colored hands, however, suggesting inhibition related to higher-level identity constructs.

Brain areas involved in social cognition may work in consort with the frontal lobes to select simulations that are congruent with an agent's goals. For example, early motor system resonance is lower while preparing to counter-imitate than to imitate (Cross & Iacoboni 2014), can be modulated by likeability of the actor (Sobhani et al 2012), and is reduced when the participant is treated unfairly by the actor (Aragón et al 2013). Nonconscious mimicry is heightened when the subject desires to desires social connection or rapport, suggesting that social goals modulate simulation (Lakin and Chartrand 2003; Aragón et al 2013). Furthermore, movement-congruency effects are moderated by whether the actor and observer share the same action intention, demonstrating a layered control mechanism over action simulation (Ondobaka et al 2012). The supplementary motor area (SMA) may also provide such control; within the population of mirror neurons in the SMA, a subpopulation

of neurons respond with excitation during action and inhibition during action observation (Mukamel et al., 2010).

## Motor Imagery

**Overlapping representations of motor actions and imagery**—Our understanding of motor imagery follows the widely accepted description of Richardson (1969): “the quasi-sensory and quasi-perceptual experiences of which we are self consciously aware and which exist for us in the absence of those stimulus conditions that are known to produce their genuine sensory or perceptual counterparts...” Motor imagery is thus the subjective experience of quasi-movement, in the absence of corresponding overt movement (though small muscle activations may occur). Motor imagery activates brain areas similar to those used in motor production (for a review, see Jeannerod & Frak 1999; Oosterhof et al., 2012), including primary motor (Porro et al 1996; Roth et al 1996), premotor, and parietal regions, and the supplementary motor area and cerebellum (Stephan et al 1995; Decety et al 1994; Filimon et al., 2007; Gerardin et al 2010). Some studies have observed a greater response to motor imagery than to motor production in the bilateral premotor, prefrontal, and supplementary motor areas, left posterior parietal cortex, and the caudate nuclei (Gerardin et al 2010), as well as the right superior posterior parietal lobe (Harris & Miniussi 2003). Motor imagery also exhibits somatotopy (Ehrsson et al 2003; Lorey et al 2013). A direct effect of motor imagery on motor production is evidenced by increased corticospinal excitability of motor neurons in response to imagined movements (e.g. Fourkas et al 2006; Li 2007; Bakker et al 2008; Liepert & Neveling 2009) and by the disruptive effect of TMS over the motor cortex on mental rotation tasks (e.g. Ganis et al 2000).

**Interactions Between Action and Motor Imagery**—The interaction between motor feedback and motor imagery is frequently demonstrated through the mental rotation paradigm (Shepard & Metzler, 1971). Multiple studies in which subjects mentally rotate two drawings have found that response times increase monotonically with the angle of discrepancy between the two images (Petit et al 2003), suggesting that subjects use motor imagery to simulate rotating the images. Similarly, Parsons showed that reaction time correlated with ease of movement from the participant's current position to the position of the pictured hand (Parsons 1994; Parsons 1987). This effect of body position on mental rotation has been shown to be effector-specific (Ionta et al 2007), demonstrating that the influence of motor activity on motor imagery depends on the congruence between motor state and motor imagery. Study participants have been unable to learn new motor movements solely through motor imagery (Mulder et al 2004), however, suggesting that motor imagery depends on existent motor representations. Motor imagery can facilitate motor production. For example, motor imagery has been used to improve strength, speed of action, range of motion, and posture in healthy individuals and athletes, as well as skilled actions in nursing and surgery (Dicksten & Deutsch, 2007). Motor imagery has also been shown to aid in rehabilitation of motor movement in patients suffering or recovering from stroke, spinal cord injury, and Parkinson's disease (Zimmermann-Schlatter 2008; Oh et al 2010; Tamir et al 2007; Dickstein & Deutsch, 2007). Repeated motor imagery practice increases motor-related activation of premotor, primary motor, and superior parietal regions in stroke patients (Page et al 2009a). In a patient with profound hemiplegia, daily motor



imagery practice led to cortical reorganization, including increased activity in parietal, motor, and SMA areas contralateral to the paralyzed limb (Johnson-Frey et al, 2004). Motor imagery can interfere, however, with production of incongruent movements. Hall et al (1995) had participants practice a simple motor task and then practice an interfering movement- either overtly, or through imagery alone. Imagined and overt practice with the conflicting movement produced similar degrees of interference with retention of the original motor pattern, suggesting strong similarity in the processing of sensorimotor production and imagery.

Motor imagery also appears to be affected by the anticipated sensory consequences of an imagined movement. The forward model of motor control posits that efference copies of motor commands are sent to the parietal lobes and are used to generate predicted sensory feedback from the planned action (e.g. Wolpert and Miall 1996). Comparison between the predicted sensory feedback and actual sensory feedback is used to fine-tune movements (e.g. Wolpert 1997). Indeed, Coslett et al (2010) report that patients with chronic shoulder or arm pain conditions are slower than controls to judge the laterality of hand drawings when the implied motor imagery involved painful amplitudes of rotation. This suggests that parietal cortex regulates motor imagery through simulation of the anticipated sensory consequences of an imagined movement.

**Processes that Regulate Motor Imagery**—To learn about the regulation of motor imagery, it is again useful to consider what happens to motor imagery when motor production is disabled. Silva et al (2011) studied mental rotation in patients with temporarily anesthetized arms. The patients performed poorly, but improved greatly when allowed to observe their anesthetized arm. This suggests that feedback from the peripheral motor system plays an important role in motor imagery, perhaps by providing information about limb position. It also suggests that visual information can supply important information, which may explain why motor referral (with its visual input) is less affected by deafferentation. Permanent deafferentation shows a similar effect. Nico et al (2004) found that upper limb amputees (the majority of whom reported phantom sensations) were impaired on an upper limb mental rotation task, but showed a similar response pattern to that of control subjects: showed slower response times, and more errors for anatomically difficult postures. Interestingly, wearing a static prosthesis interfered with motor imagery much more than a functional prosthesis. This suggests that the motor affordances of a functional prosthesis may be incorporated into a patient's body schema. These studies suggest some dependence of motor imagery on motor and visual feedback; motor imagery may be constrained when motor and visual feedback are unavailable.

In some patients with deafferentation, however, motor imagery is well preserved. Using fMRI, Erslund et al (1996) found that a patient with a phantom right arm activated contralateral motor cortex in response to mental imagery of finger tapping of the phantom. Single neuron recordings performed in amputees during imagined movements of the phantom showed similar activation of neurons in the cerebellum, basal ganglia, and ventral caudal somatic sensory nucleus to control patients imagining arm movement. This activation may relate to planning movements and their predicted sensory consequences (Anderson et al 2010). Indeed, Lotze et al (2001) found that patients with a phantom limb showed

significantly *higher* motor and sensory activation than controls during motor imagery. Most of the patients also reported a subjective feeling of movement in their phantom limb. Lotze et al attribute this finding to the high level attention paid by patients to pain and sensation in their phantom arm. Another possibility, however, is that motor imagery, like motor referral, is stronger in the absence of motor feedback. This suggests a tonic suppression of motor imagery by motor feedback.

In sum, phantom limbs appears to have a deleterious effect on motor imagery in some cases, but preserve or facilitate it in some patients with phantom limbs. Several factors may be involved in these divergent outcomes. First, the phantom limb patients studied by Lotze et al (2001) had been amputated for a mean of 17.3 years, while the amputees studied by Nico et al, had been amputated for a mean of only about 5.5 years. There may have been differences in the mobility of the phantom limbs in each study, as well as the degree of difficulty of the motor tasks. Finally, while Nico et al's task required implicit simulation, Lotze's demanded explicit simulation. Raffin et al (2012) has shown that attempting to make “real” versus “imagined” movements of phantom limbs results in different neural activations, similar to the differing activations observed in response to real versus imagined movements of intact hands. Raffin et al also showed, however, that imagery for phantom limbs and intact limbs produced similar levels of brain activation. Given these mixed findings, we suggest that strong motor imagery depends on intact central motor representation of a movement, but not on online motor feedback. We also suggest that it requires a representation of limb position that is compatible with the imagined movement.

Another way to look at interactions between motor production and motor imagery is to examine cases of central motor damage. Johnson et al (2002) investigated motor imagery in patients who had suffered cerebral vascular incidents damaging motor ability but sparing parietal and frontal areas involved in motor simulation. Compared to recovered controls, the patients were unimpaired on imagery involving the affected limb. Unexpectedly, however, the patients performed *more* accurately in their hemiplegic limb. Johnson et al suggest that this ‘hemiplegic advantage’ may be related to increased motor planning effort in the immobilized limb. Another possibility, however, is that in the absence of motor feedback from the limb, imagery might be strengthened. How can the hemiplegic advantage (Johnson et al 2002) be reconciled with the inferior performance of healthy individuals with anesthetized arms on mental rotation (Silva et al 2011)? One possibility is that hemiplegia may disrupt proprioceptive monitoring- eliminating conflict with the motor imagery-while patients with anesthetized limbs might maintain proprioceptive representations of the arm prior to the procedure that would conflict with imagined movements. Indeed, many patients undergoing brachial plexus blocks experience a static “phantom arm” (e.g. Gentili et al 2002). Motor feedback may thus inhibit incongruent motor imagery. When motor feedback is reduced, motor imagery may be enhanced, unless the motor system clings to a sensorimotor memory of limb position that is in conflict with the imagined movement. Motor damage that reduces proprioceptive monitoring may remove this impediment, strengthening motor imagery.

Conversely, several groups have suggested that motor imagery inhibits motor production (e.g. Lotze et al 1999, Decety 1996, & Jeannerod 1994). Deiber et al (1998) report that when



participants moved their finger, activity increased in primary motor areas and decreased in the inferior frontal cortex, compared to when they imagined watching their finger move. The authors therefore propose that the inferior frontal cortex plays a role in suppression of motor production during motor imagery. Parietal areas may also suppress production of imagined movements. Schwoebel et al (2002) report that a bilateral parietal lesion patient, CW, unwittingly executed left-handed motor movements that he imagined. Schwoebel et al suggest the CW's parietal damage interfered with a parietal lobe mechanism by which motor imagery normally inhibits its own motor output. Schwoebel et al also suggest that CW was unaware of proprioceptive feedback from his movements due to the normal suppression of sensory information during motor imagery. Evidence for such suppression exists in the visual domain; Craver-Lemley & Reeves (1992) report reduced visual sensitivity during visual imagery. These findings suggest that frontal and parietal brain areas monitor the proprioceptive consequences of motor imagery, and suppress overt production of the imagined movement.

The SMA may help the brain from confusing motor planning and motor imagery. Grafton et al (1996) employed positron emission tomography (PET) imaging during observation or imagery of hands grasping and suggested that activation in the SMA and cerebellum distinguishes real movement from imagined movement. Similarly, Grèzes & Decety (2001) report additional activation of pre-SMA and dorsolateral frontal cortex in motor production versus motor imagery; these areas may relate to prospective memory for action planning. Motor imagery also shows activation of ventral premotor cortex that might be explained by verbal mediation.

The parietal lobes may also play a role in keeping motor planning and motor imagery distinct by comparing sensory prediction with the sensory feedback from motor movements. Another reason for the lesion patient CW's anosognosia for his imagery-induced movement (discussed above) may be a confusion of sensory prediction and actual sensory feedback caused by his bilateral parietal lesions. Without being able to recognize that he was producing or planning to produce his imagined movements, he could not inhibit their actual production. Indeed, illusory movements of phantom limbs may be so vivid because of a lack of real motor feedback distinguishing the sensation of motor imagery from the sensation of actual movement (Ramachandran & Hirstein 1998). In CW, actual sensory feedback from his imagery-induced movements might be construed as motor prediction; in phantom limb patients, predicted motor feedback might be mistaken for actual feedback. This suggests that predictive feedback also plays an important role in distinguishing real movement from motor imagery.

Little work has investigated regulation of motor imagery by social or motivational factors. However, it is likely that the strength of motor imagery depends upon attention and upon social-emotional factors. For example, it may be more difficult to imagine the actions of a person we dislike or disidentify with, in the same way that we mirror them less in person (Aragón et al 2013).

## 2. The Sensory System

Recent research demonstrates that sensory observation and sensory imagery can activate the somatosensory system, sometimes even leading to a feeling of touch (Fitzgibbon et al, 2012). Sensory referral (somatosensory activation by observed sensation) and sensory imagery (imagery of tactile sensation) have been explored in less detail than motor referral and motor imagery. One reason for this may be that sensory referral does not typically give rise to conscious qualia of touch. Another reason is that somatosensory perception is not externally observable in the way that motor activation is (e.g. by measurement of muscle activation). A number of studies, however, demonstrate strong functional overlap and interaction between somatosensation and sensory simulation. We will review these studies and then consider how the brain regulates sensory simulation, drawing parallels to regulation of simulation in the motor system.

### Sensory Referral

**Overlapping representations of somatosensation and observed touch—**A somatosensory analog to the mirror neuron system would provide a mechanism for mapping observed touch onto first-person somatosensory representations (e.g., Bradshaw & Mattingley, 2001; Rizzolatti & Craighero, 2004; Damasio and Meyer, 2008). Indeed, cross-modal links exist between vision and touch at early stages of sensory processing (Posner & Peterson 1990). Sensory referral is the activation of the somatosensory system in response to the observation of touch to another person. Sensory referral may be unconscious, or it may give rise to a conscious quale of touch. For example, tactile detection is faster while viewing a congruent body part (Tipper et al 1998; Kennet et al 2001; Rorden et al 1999; Schaefer et al 2005). This effect has been localized by TMS to the primary somatosensory cortex (S1) (Fiorio & Haggard 2005), where visual input may sharpen somatosensory receptive fields (Haggard et al 2007). S1 is also richly connected with the mirror-neuron rich premotor and posterior parietal cortices (Driver and Spence, 2000; Rockland and Ojima, 2003), which may mediate the crossmodal modulation of S1 via back-projections. Brain imaging studies corroborate the neural overlap of somatosensory processing and touch observation. Overlapping adaptation in S1 has been observed during action observation and action execution (Dinstein et al 2007), suggesting sensory mirror regions, and possibly sensory mirror neurons. Furthermore, vicarious activation of Brodmann Area 2 (BA2) to observation of hand and mouth actions matches the somatotopy of this sensory area (see Keysers et al 2010), suggesting functional overlap of observation and sensation. Primary somatosensory cortex (SI) activity has been identified during observation of touch in some studies (e.g. Blakemore et al 2005; McCabe et al 2008), though not in others (e.g. Keysers et al 2004); intentionality of the observed touch may affect the recruitment of S1 (Ebisch et al 2008). BA1 and BA2 appear to track the agent of touch, while secondary somatosensory cortex (SII) responds more to observing the recipient of touch (Keysers et al 2010; Bufalari et al 2007). More recently, Kaplan & Meyer (2012) used multivariate pattern analysis to show common neural patterns across individuals during touch observation, with stimulus-specific patterns of activity in sensorimotor networks, and Kuehn et al (2013) observed increased posterior S1 activation during 7 Tesla fMRI while participants observed another person's hand receiving touch. Transcranial magnetic stimulation (TMS) has also recently provided

causal evidence that sensory cortex is modulated by observed touch (e.g. Bolognini et al 2011). Vicarious responses are also seen in response to observed pain. Responses to observed pain overlap strongly with the pain matrix, including the insula, somatosensory cortex, anterior midcingulate cortex, periaqueductal gray, and supplementary motor area (Decety et al 2008). Similarly, vicarious responses to emotional expressions include brain areas involved in the experience of pain such as the insula and cingulate cortex (Bastiaansen et al., 2009).

**Interactions Between Somatosensation and Observed Touch**—The effect of sensory referral on somatosensation is strikingly demonstrated by the rubber hand illusion (RHI). When a rubber hand and a participant's occluded hand are spatially aligned and stroked in synchrony, many participants begin to feel that their own sensation is arising directly from the rubber hand (Botvinick & Cohen 1998). Sensory referral in the RHI displaces proprioceptive judgments of limb position towards the rubber hand in proportion to the depth of illusion experienced. Similarly, participants react faster to touch when they watch another person (but not object) receive anatomically congruent touch (Thomas et al, 2006). Watching movies of others scratching often induces feelings of itchiness (Papoiu et al 2011; Holle et al 2012), and activates many of the brain areas associated with itch perception. In one case, a construction worker reported severe pain in his right foot after jumping onto a 15cm nail- even though the nail passed directly between his toes without injuring his foot (Fisher et al 1995). Sensory referral can also interfere with tactile processing. Viewing incongruent touch to another person's hand, for instance, interferes with spatial touch perception on one's own hand (Maravita et al, 2002). These studies clearly demonstrate a somatotopic effect of sensory referral (and related types of visual feedback) on somatosensory processing.

There is little research on the converse effect, the effect of touch on sensory referral. However, the rubber hand illusion is strengthened when touch to the participant and rubber hand are spatially and temporally aligned, suggesting that congruent sensation facilitates sensory referral (Tsakiris et al 2007). In addition, observing- but not hearing- speech increases the neural response to touch on the lips (Möttönen et al, 2005). Mouth movements strongly suppress this vicarious S1 response, however, suggesting that sensorimotor feedbacks inhibit sensory referral in SI. Thus there seems to be mutual inhibition between somatosensation and sensory referral.

**Processes that Regulate Sensory Referral**—What is the relationship between sensory feedback and sensory referral? Interestingly, there is evidence- as in the motor system- that amputees experience heightened sensory referral in their phantom limb, suggesting tonic inhibition of sensory referral by afferent sensation. When an amputee superimposes his or her intact arm onto his or her phantom in a mirror, touching the intact arm gives rise to referred sensation in the phantom (Ramachandran et al, 1995; Ramachandran & Rogers-Ramachandran 1996). Sensations can also be referred from the experimenter's limb to the patient's phantom; indeed, watching another person's limb being massaged can reduce reports of pain in patients with phantom pain (Ramachandran & Brang 2009; Weeks & Tsao 2010), and observing illusory touch can significantly reduce pain even

in phantom limb patients for whom *motor* mirror therapy has failed (Schmalzl et al, 2013). Goller et al (2013) reported mirror-touch synaesthesia (sensory referral) in about one third of tested amputees; sensations were more intense when real bodies were observed, and for observation of painful touch. This strong sensory referral suggests that afferent sensation may normally inhibit sensory referral. Patients with anesthesia resulting from stroke also report increased sensory referral: touching the intact hand refers sensation to the anesthetized hand (Sathian, 2000). In this case, an absence of sensation from the anesthetized hand may disinhibit transcallosal input. Similarly, patients with anesthetic blocks of the brachial plexus (for orthopedic surgery) have been found to exhibit more sensory referral to the anesthetized arm than to the non-anesthetized arm, supporting the theory of inhibition of simulation by afferent sensation (Case et al 2010). Similarly, heightened mirror touch-confusion has been observed in healthy volunteers from a topical anesthetic cream, suggesting that sensory referral may be disinhibited rapidly when afferent sensation is reduced (Case et al 2013).

As in the motor system, aberrant cases of sensory referral can reveal mechanisms of normal neural regulation of simulation. Bradshaw & Mattingley (2001) report an anecdotal case of a patient who had suffered head trauma affecting the parietal lobes and subsequently exhibited strong, automatic sensory referral of pain, as well as hyperaesthesia. The patient experienced instantaneous discomfort upon seeing minor injury, but only when the injury was sudden. The patient's widow reported him saying "don't do that (meaning not to show him suddenly); he actually felt it" (in Bradshaw & Mattingley, correction to letter). This hyper-referral may have resulted from decreased or delayed frontal inhibition of the sensory mirror system, allowing unanticipated sensory pain referral to be experienced consciously. Similarly, as in the motor system, transcallosal inhibition may provide another source of modulation of sensory referral. Takasugi et al (2011) find that about a quarter of participants experience sensory referral from observing their contralateral arm in a mirror, but about 85% experience sensory referral when observing the arm of another person in the mirror, suggesting that transcallosal signals of one's own motor activity inhibit intrapersonal sensory referral. Deactivation of ipsilateral SI is common in response to unilateral touch, (Hlushchuk & Hari 2006), so transcallosal inhibition of sensory referral may be affected through the same mechanism.

If sensory neurons fire when we observe touch, why do we not actually feel touch "quale" when we observe touch? How do we avoid confusion between our own sensation, and the sensation of another person? de Vignemont discusses the dilemma the brain faces in needing to simultaneously solve both the correspondence problem (map another body and its sensations onto your own) and the identity problem (determine to whom these mapped sensations belong). Sensorimotor feedback- unique to the self- may afford this distinction (de Vignemont 2014). Brodmann Area 3 (BA3) in S1 may play a role in distinguishing between direct and vicarious somatosensation, as only mirror-touch synesthetes, who confuse actual and vicarious touch, activated BA3 in response to observing touch (Blakemore et al 2005). Similarly, Schaefer et al (2006) report that activity in SI dynamically shifts inferiorly during synchronous touch compared with asynchronous touch during touch observation; this shift positively correlated with participants' reports of sensory

referral. SI may thus be modulated by brain areas involved in source attribution, or by multisensory synchrony that contributes to inferences about body ownership.

Self-identification may also regulate sensory referral. In touch-confusion paradigms where a participant is touched on the face while viewing touch to another person's face, the interference of sensory referral (number of touch confusions) is greatest when the model is perceived as similar to the subject (Banissy & Ward 2013). Touch-confusion may thus result from errors in self-other monitoring, resulting in disinhibition of the sensory mirror response. This suggests a modulatory role of brain regions involved in identifying the sensation as belonging “self,” such as the insula. Activation of the posterior insula is related to strength of the RHI. In addition, greater proprioceptive drift in the RHI (indicative of greater illusion) correlates with reduced S1 and S2 activity but heightened right posterior insula activation. This suggests involvement of the posterior insula in perceived ownership of a body part (Tsakiris et al., 2007). The right posterior insula has been related to egocentric representation (Fink 2003), self-recognition (Devue et al., 2007), and body ownership (Baier & Karnath, 2008). These areas parallel the role of the right inferior parietal cortex and temporo-parietal junction in inhibiting motor imitative response and observing oneself being imitated (Brass & Heyes 2005, Decety et al, 2002).

Social goals and affiliations also appear to regulate the simulation of vicarious touch and pain. Acupuncturists, who administer pain for therapeutic purposes, show reduced vicarious pain response in the anterior cingulate cortex and anterior insula (Cheng et al., 2007), perhaps through frontal inhibitory control. Simulation of another's pain is enhanced for individuals of one's ethnic in-group (Rie anský et al 2014). Simulation of non-painful touch also appears to be regulated by a number of social, emotional, cognitive factors (Bufalari & Ionta 2013).

Finally, touch synaesthesia may reveal aspects of normal regulation of sensory referral. Strong sensations of touch in response to observed touch are reported in a rare form of congenital synesthesia called “mirror-touch synesthesia” (e.g. Banissy et al, 2009). This observation is corroborated by higher rates of touch-confusion errors in mirror-touch synesthetes than in non-synesthetes (Banissy & Ward 2007). Mirror-touch synesthetes show slowed reaction times when actual and observed touch are incongruent, suggesting an interference effect of sensory referral on sensory discrimination. However, synesthetes are not faster than controls when these stimuli are congruent, suggesting that the facilitation and interference effects of sensory referral may depend upon different neural processes, such as a failure to recognize a recipient of touch as being not-self. Blakemore et al (2005) compared one mirror-touch synesthete to 12 non-synesthetes and found higher activation in the synesthete during observation of touch in SI, SII, left premotor cortex, and anterior insula. Watching touch to others also caused changes in mental representations of self in mirror-touch synesthetes, supporting the theory that differences in mapping of sensation as “self” or “other” may determine whether sensation is experienced consciously (Maister et al 2013, Banissy & Ward 2013). Indeed, synesthetic touch is strongest for touch to real bodies and weaker for dummy bodies or pictures of bodies (Holle et al, 2011). Mirror-touch synesthesia may constitute an extreme version of normal sensory referral that has exceeded (or circumvented) the threshold for consciousness (Fitzgibbon et al, 2012). Indeed, there are

reports that hyperactivity in somatosensory mirror areas induced by pain or trauma, or experimentally by transcranial direct current stimulation (tDCS), may heighten response to observed touch and pain (Fitzgibbon et al., 2010; Bolognini et al 2013).

## Sensory Imagery

### **Overlapping representations of somatosensation and sensory imagery—**

Sensory imagery- the imagining of sensation- is difficult to study in isolation; few measures other than self-report have been developed to determine whether a person literally feels an imagined sensory stimulus. In addition, the boundary between sensory imagery and sensory referral is not distinct. Armel & Ramachandran (2003) demonstrated sensory referral from a table to participants' hands (via synchronous stroking, as in the RHI); the referral was strengthened if the subject simultaneously engaged in imagery, imagining that the table was their hand. It is unclear whether the sensory referral resulted from visual input, or from imagery biasing the interpretation of the visual input. Similarly, a PET study conducted by Rauch and colleagues (1995) to examine the neural basis of phobic symptoms found a significant somatosensory activation, even though the provocative stimuli were purely visual (e.g. a live spider in a jar). The authors suggest that the visual stimuli may have induced vivid tactile imagery, as all participants reported both tactile and visual imagery.

Despite these challenges, several studies provide insight into the brain correlates of sensory imagery. Primary and secondary somatosensory areas are often recruited during tactile imagery, and partially overlap with the areas that respond to touch. Using fMRI, Yoo et al (2003) found that tactile imagery for the hand engaged contralateral S1 and S2, left parietal lobe, left inferior frontal gyri, left dorsolateral prefrontal area, left precentral gyrus, left insula, medial frontal gyrus, left thalamus, and the putamen. Tactile expectation may also be considered a type of imagery, as it involves a sensory stimulation of the expected touch that often invokes imagery. Studies of tactile expectation thus provide some insight into imagery. Anticipation of tickling generates brain activation similar to that of actual tickling, including activation of the contralateral primary sensory cortex, bilateral areas in the inferior parietal lobules, SII, right anterior cingulate cortex, and areas in the right prefrontal cortex (Carlsson et al 2000). In addition, prediction of a sensory stimulus in the near future improves the speed and accuracy of sensory response (Posner & Peterson 1990) and modulates activity in SI (van Ede et al, 2010; Langner et al 2011). Langner et al (2011) suggest that top-down attentional mechanisms modulate signal-detection of touch in sensory cortices by modifying baseline levels of activity.

Sensory imagery can also cause physiological response. For example, orgasm from mental imagery alone can produce increases heart rate, systolic blood pressure, pupil diameter, pain detection threshold, and pain tolerance threshold comparable to those produced by self-stimulation (Whipple et al 1992). Sensory imagery can also affect body temperature. Kojo (1985) asked participants to imagine holding their hand in hot or cold water, and found that participants' skin temperature changed significantly in the congruent direction during trials that the subject reported successful imagery. Maslach et al (1972) controlled for the possibility that this association was correlational rather than causal by asking subjects to simultaneously change their skin temperature on both hands, in opposite directions.



Participants who had hypnosis training were able to achieve this. Interestingly, all participants believed they had successfully created bilateral temperature differences. This suggests that temperature imagery may have changed temperature perception, without changing actual skin temperature. Sensory imagery has also been shown to modulate pain. For example, Johnson et al (1998) found that imagery of neutral or pleasant events increased pain thresholds, and Van Tilburg et al (2009) obtained long-term sustained pain reduction in children with functional abdominal pain through guided imagery.

**Interactions Between Somatosensation and Sensory Imagery**—Sensation affects sensory imagery. For example, Atance and Meltzoff (2006) studied how three- to five-year-old children's preferences for future pretzel-eating were influenced by their current level of thirst (manipulated by feeding them pretzels). Despite children's overwhelming desire for pretzels in the baseline condition, thirsty children chose water for their current snack- but also when asked about a snack planned “for tomorrow.” The children's thirst sensation interfered with accurate sensory simulation of their future sensory states. This interference did not depend on children's age, and all understood “tomorrow,” suggesting that the failure was not directly dependent on theory of mind or executive control abilities that are actively developing in this age range. In fact, similar findings have been obtained in adults; Nisbett and Kanouse (1969) and Gilbert et al (2002) both found that hungry shoppers purchase more food than those who are not hungry. If truly divorced from frontal lobe inhibition, developmental differences in simulating the future might reflect gradual development of the mutual inhibition between sensory perception and sensory simulation that help separate reality from imagination. Indeed, children have more difficulty with source monitoring and are more likely than adults to confuse imagined actions with their own real actions (Foley & Johnson 1985).

Sensory imagery also affects sensation. Perky (1910) reported that when participants were asked to describe common objects while dim projections of the objects were surreptitiously presented, participants reported perceiving only imagery: they remained unaware of the real visual stimulus being shown. Similarly, Segal & Fusella (1970) found reduced sensitivity to auditory and visual stimuli while subjects imagined pictures and sounds; intramodal imagery interfered more than intermodal imagery. Unfortunately, few little comparable data are available in the somatosensory domain. Facilitation of sensory perception through imagery is complicated to assess, as a stronger tactile percept is not necessarily a more accurate percept, and vice versa. However, there is some evidence that imagery can affect sensation. Talking about an itch, for example, tends to make a listener feel itchy and scratch more (Niemeier & Gieler 2000). The contagion of physical distress through seeing, hearing, or reading about another person suffering is surprisingly common (Morse and Mitcham, 1997). Pleasant sensations can also be enhanced through imagery. For example, the pleasantness of caress and corresponding touch-evoked activation in S1 are enhanced when the apparent (implied) gender and attractiveness or the caresser is manipulated (Gazzola et al 2012). Thinking about touch can also selectively facilitate response time to tactile stimuli (Anema et al 2012).

**Processes that Regulate Sensory Imagery**—There is little research on the effect of deafferentation on sensory imagery. However, Hugdahl et al (2001) have demonstrated activation of sensory cortex and sub-cortical pain pathways when an upper limb amputee imagined moving his fingers in a way that would cause pain, suggesting that sensory imagery is not abolished by the removal of sensory feedback. It is not clear whether or not sensory imagery might be enhanced by deafferentation.

The prefrontal cortex may play an important role in modulation of sensory imagery. The prefrontal cortex supports task performance by exciting task-relevant information processing and inhibiting irrelevant information (Knight et al 1999); patients with damage to prefrontal areas have difficulty inhibiting task-irrelevant information. Interestingly, these patients also exhibit enhanced primary somatosensory cortical responses to distracting sensory information, suggesting that prefrontal damage disrupts sensory inhibition or sensory gating. Similarly, Yamaguchi et al (2006) report heightened somatosensory evoked potentials (SEP) in a patient with frontal alien hand behavior following medial frontal lobe damage; the frontal lobe damage likely disinhibited the patient's somatosensory response.

Hypnosis is another phenomenon that implicates the frontal lobes in regulation of sensory imagery. Hypnotic suggestions can generate strong sensory imagery that blurs the line between perception and reality (e.g. Schweiger & Parducci 1981; Santarcangelo et al 2005). Hypnosis may decrease frontal cognitive control (e.g. Wagstaff et al 2007) and disinhibit sensory areas, making participants more susceptible to suggestion- or it may decrease activation of areas like the medial frontal lobe that are implicated in distinguishing real and imagined perceptual events (Ku et al 2008). Some studies have found a positive correlation between hypnotizability and imagery ability (e.g. Hargadon et al 1995; Paoletti et al 2010), while others have not (e.g. Kogon et al 1998). Further, highly hypnotizable subjects have achieved stronger tactile imagery than other subjects (Carli et al, 2007), and individual differences in hypnotizability are linked with efficiency of the attentional system in the frontal lobes (Egnera et al 2005). Finally, hypnosis increases pain-related brain activity generated by imagery of pain (Derbyshire et al, 2004). Activation of the right dorsolateral prefrontal cortex, insula, and anterior cingulate cortex predicted pain-related activation in the secondary somatosensory cortex (SII) (Raij et al 2009). These studies suggest that hypnosis may strengthen sensory imagery by decreasing inhibitory control from the frontal lobes.

Tactile hallucinations provide another window into the normal regulation of sensory imagery. One type of chronic tactile hallucination is known as *Dermatozoenwahn*- a feeling of bugs swarming crawling, and jumping on the skin. SPECT imaging of patients with *Dermatozoenwahn* during active tactile hallucination showed decreased frontal activity and inferior temporal activity, coupled with increased activity in the anterior basal ganglia (Musalek et al 1989). Musalek et al relate their finding to Jackson's (1932) hypothesis that hallucination results from decreased inhibition of basal structures by upper cortical structures. Other studies merely show activation of sensory regions. Shergill et al (2001) studied a single patient with fMRI and found that the somatic hallucinations were associated with the primary somatosensory cortex, posterior parietal cortex, and the thalamus. Nemoto et al (2010) studied five patients with delusional disorders during somatic hallucination and

found hyperperfusion of left somatosensory cortex and right paracentral cortex. What happens to somatic hallucinations when sensory processing regions are damaged? Braun et al (2003) reviewed studies of single-modality hallucination after focal brain lesions and reported strong concordance between lesion area and sensory modality of hallucination; they suggest that hallucinations after focal brain damage are caused by compensatory over-activation of neural tissue proximal to the injury. Loss of sensory brain tissue may release inhibition of sensory cortex and cause spontaneous activity resulting in hallucination, despite patients' awareness of the illusory nature of the hallucination. Perhaps the normal function of the frontal lobes in these patients may underlie their continued ability to discriminate hallucination from reality.

## Summary

Research on common coding in the human mirror neuron system has turned up strong evidence for overlapping neural representations of motor production, motor imagery, and action perception. We review interactions between these mingled processes and explore how these interactions are regulated. We also extend this logic to the somatosensory domain and the putative somatosensory mirror system. Here we also suggest that there is evidence for mutual interaction between somatosensation, observed touch (sensory referral), and sensory imagery. Most frequently, touch enhances sensory referral and imagery if it is similar (as in the rubber hand illusion; e.g. Tsakiris et al 2007), and detracts from the simulation if it is dissimilar (as in the interference of thirst on simulation of desire for food; Atance et al 2006). Conversely, sensory simulations influence the perception of touch. Observing insects can induce sensations of itch (e.g. Rauch et al 1995), and observing touch can interfere with perception of dissimilar touch on ones own skin (e.g. Maravita et al, 2002).

Overlapping representation of perception and action implies that the processing of actual, imagined, and referred movements and sensation must compete for control of behavior, physiological response, and conscious representation. These interactions therefore must be carefully regulated in order to maintain a grasp on reality. Counterintuitively, we suggest that deafferentation often *increases* visual referral of movement or sensation- most likely due to a push-pull system of activation-deactivation. This suggests that sensorimotor feedback normally inhibits simulation. Removing this feedback may also remove interference effects caused by dissimilar movements and sensations. In addition, evidence from imaging studies and patient reports suggests that frontal, parietal, and transcallosal inputs flexibly suppress simulations that interfere with current sensorimotor goals, while inferior parietal and superior temporal areas may influence the strength of sensorimotor simulation in accordance with social or self-identification with a goal or with an actor. When areas involved in regulation are damaged, or when sensorimotor activity is removed, simulation may paradoxically be disinhibited and strengthened. More research is needed to fully evaluate these effects.

A number of studies now suggest that sensorimotor imagery and perception affect our sensation, actions, and physiology. Pfister et al (2011) describe this effect in terms of competition between endogenous and exogenous actions for control of our perception and behavior. Endogenous actions are internally generated, while exogenous actions are quick,

environmentally driven responses to external cues. While imagery and action observation are not solely exogenous, they present a similar problem: without proper control, they may lead to behaviors inappropriately linked to present goals or circumstance, as in the case of unrestrained imitation, or unanchored to their source, as in the case of hallucination. The influence of simulation must be moderated by our needs, preferences, and limitations.

## Future Directions

Many questions remained unanswered about the influence and regulation of sensorimotor simulation. First, most researchers have considered sensorimotor imagery or observation in isolation. Given their neural overlap, it is likely that they interact with one another. This raises questions about how simulations are prioritized versus suppressed, and the extent to which these processes are under voluntary control. Sensory and motor referral are by definition automatic processes, yet they are strongly influenced by an agent's conscious goals. Voluntary motor imagery practice, for example, enhances motor ability (e.g. Dickstein & Deutsch, 2007), and voluntary imagery enhances sensory referral (e.g. Armel & Ramachandran, 2003). More investigation is needed to examine the roles of volitional attention and top-down executive control in influencing the fate of sensorimotor simulations. In addition, many questions remain about the mechanism of interaction between various sensorimotor processes. The mutual influence of simulation and “real” movement or sensation on one other does not distinguish whether their interaction arises from activation of identical neurons or through excitatory and inhibitory connections between neighboring neural representations. Because almost all work on the mirror neuron system in humans is conducted through behavioral and neuroimaging experiments that interrogate populations of neurons, it is difficult to say whether mirror neurons themselves- or mirror mechanisms- subserve the interactions described in this review.

Future research is also needed to understand the regulation of sensorimotor simulation across development and in health and disease. Understanding interactions between simulation and “real” sensorimotor activity may provide greater insight into development of empathy and cognitive control. This balance may also underlie individual differences in imagery ability, ability to learn by imitation, and the ability to plan for counterfactual circumstances. Further, understanding the impact of brain lesions and disease on sensorimotor simulation may lead to new insights in sensorimotor rehabilitation. Motor imagery and observation are helpful for rehabilitation in a wide range of conditions, and further knowledge about the regulation of simulation may help to optimize their rehabilitative effects as well as improve motor learning in healthy individuals. Finally, more research is needed to determine how somatosensory simulation is regulated and harness this information to understand and treat conditions involving abnormal sensation or pain. For instance, methods to temporarily reduce inhibitory cognitive control, such as hypnosis, may enhance the therapeutic effect that sensory imagery has on pain (e.g. Johnson et al 1998; Van Tilburg et al 2009), and therapies combining imagery and referral might be more successful than either alone in achieving specific sensorimotor goals. The influence of social identification on strength of simulation might also be harnessed in novel ways to increase sensorimotor goals through simulation.

## Acknowledgements

The authors thank Pat Churchland, Piotr Winkielman, Claire Laubacher, and M Catherine Bushnell for assistance and helpful conversations. The first author thanks the University of California, San Diego and the National Center for Complementary and Integrative Health (NCCIH) for support during the preparation of the manuscript. The views presented in this paper are solely those of the authors and do not necessarily reflect views of NCCIH.

## References

- Altschuler, EL.; Vankov, A.; Wang, V.; Ramachandran, VS.; Pineda, JA. Person see, person do: human cortical electrophysiological correlates of monkey see monkey do cells.. Poster session presented at the 27th Annual Meeting of the Society for Neuroscience; New Orleans, LA. 1997.
- Anderson WS, Weiss N, Lawson H,C, Ohara S, Rowland L, Lenz FA. Demonstration of motor imagery movement and phantom movement-related neuronal activity in human thalamus. *Neuroreport*. 2010; 22(2):88–92. [PubMed: 21150804]
- Anema HA, de Hann AM, Gebuis T, Dijkerman HC. Thinking about touch facilitates tactile but not auditory processing. *Experimental Brain Research*. 2012; 218:373–380. [PubMed: 22354100]
- Aragón OR, Sharer EA, Bargh JA, Pineda JA. Modulations of mirroring activity by desire for social connection and relevance of movement. *Social Cognitive and Affective Neuroscience*. 2013 Advance Online Publication.
- Armel KC, Ramachandran VS. Projecting sensations to external objects: evidence from skin conductance response. *Proceedings of the Royal Society B*. 2003; 270:1499–1506. [PubMed: 12965016]
- Atance CM, Meltzoff AN. Preschoolers' current desires warp their choices for the future. *Psychological Science*. 2006; 17(7):583–587. [PubMed: 16866743]
- Avenanti A, Sirigu A, Aglioti SM. Racial bias reduces empathic sensorimotor resonance with other-race pain. *Curr. Biol*. 2010; 20:1–5. [PubMed: 20036540]
- Aziz-Zadeh L, Maeda F, Zaidel E, Mazziotta J, Iacoboni M. Lateralization in motor facilitation during action observation: a TMS study. *Experimental Brain Research*. 2002; 144(1):127–131. [PubMed: 11976767]
- Baier B, Karnath HO. Tight link between our sense of limb ownership and self-awareness of actions. *Stroke*. 2008; 39(2):486–8. [PubMed: 18162622]
- Bakker M, Overeem S, Snijders AH, Borm G, van Elswijk G, Toni I, Bloem BR. Motor imagery of foot dorsiflexion and gait: Effects on corticospinal excitability. *Clinical Neuropsychology*. 2008; 119(11):2519–2517.
- Banissy MJ, Cohen Kadosh R, Maus GW, Walsh V, Ward J. Prevalence, characteristics and a neurocognitive model of mirror-touch synaesthesia. *Exp Brain Res*. 2009; 198(2-3):261–72. [PubMed: 19412699]
- Banissy MJ, Ward J. Mirror-touch synesthesia is linked with empathy. *Nature Neuroscience*. 2007; 10(7):815–816. [PubMed: 17572672]
- Banissy MJ, Ward J. Mechanisms of self-other representations and vicarious experiences of touch in mirror-touch synesthesia. *Frontiers in Human Neuroscience*. 2013; 7(112):1–3. [PubMed: 23355817]
- Bastiaansen JA, Thioux M, Keysers C. Evidence for mirror systems in emotions. *Philosophical Transactions of the Royal Society B: Biological Sciences*. 2009; 364(1528):2391–2404.
- Blakemore SJ, Bristow D, Bird G, Frith C, Ward J. Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain*. 2005; 128:1571–1583. [PubMed: 15817510]
- Bolognini N, Olgiati E, Xaiz A, Posteraro L, Ferraro F, Maravita A. Touch to see: neuropsychological evidence of a sensory mirror system for touch. *Cerebral cortex*. 2012; 22(9):2055–2064. [PubMed: 21988827]
- Bolognini N, Miniussi C, Gallo S, Vallar G. Induction of mirror-touch synaesthesia by increasing somatosensory cortical excitability. *Current Biology*. 2013; 23(10):R436–R437. [PubMed: 23701682]

- Botvinick M, Cohen J. Rubber hands ‘feel’ touch that eyes see. *Nature*. 1998; 391:19.
- Bradshaw JL, Mattingley JB. Allodynia: a sensory analogue of motor mirror neurons in a hyperaesthetic patient reporting instantaneous discomfort to another's perceived sudden minor injury? *Journal of Neurology, Neurosurgery, and Psychiatry*. 2001; 70:821.
- Brass M, Bekkering H, Wohlschläger A, Prinz W. Compatibility between observed and executed finger movements: comparing symbolic, spatial and imitative cues. *Brain and Cognition*. 2000; 44:124–143. [PubMed: 11041986]
- Brass M, Zysset S, von Cramon DY. The inhibition of imitative response tendencies. *Neuroimage*. 2001; 14(6):1416–1423. [PubMed: 11707097]
- Brass M, Derrfuss J, Matthes-von Cramon G, Von Cramon DY. Imitative response tendencies in patients with frontal brain lesions. *Neuropsychologia*. 2003; 17(2):265. [PubMed: 12803432]
- Brass M, Derrfuss J, Von Cramon DY. The inhibition of imitative and overlearned responses: a functional double dissociation. *Neuropsychologia*. 2005; 43(1):89–98. [PubMed: 15488909]
- Brass M, Heyes C. Imitation: is cognitive neuroscience solving the correspondence problem? *TRENDS in Cognitive Sciences*. 2005; 9(10):489–495. [PubMed: 16126449]
- Brass M, Bekkering H, Prinz W. Movement observation affects movement execution in a simple response task. *Acta Psychologica*. 2001; 106(1-2):3–22. [PubMed: 11256338]
- Braun CM, Dumont M, Duval J, Hamel-Hébert I, Godbout L. Brain modules of hallucination: an analysis of multiple patients with brain lesions. *Journal of Psychiatry and Neuroscience*. 2003; 28(6):432–49. [PubMed: 14631455]
- Buccino G, Lui F, Canessa N, Patteri I, Lagravinese G, Benuzzi F, Porro CA, Rizzolatti G. Neural circuits involved in the recognition of actions performed by nonconpecifics: An fMRI study. *Journal of Cognitive Neuroscience*. 2004; 16(1):114–126. [PubMed: 15006041]
- Bufalari I, Aprile T, Avenanti A, Di Russo F, Aglioti SM. Empathy for pain and touch in the human somatosensory cortex. *Cerebral Cortex*. 2007; 17:2553–2561. [PubMed: 17205974]
- Bufalari I, Ionta S. The social and personality neuroscience of empathy for pain and touch. *Frontiers in human neuroscience*. 2013;7. [PubMed: 23372547]
- Carli G, Cavallaro FI, Santarcangelo EL. Hypnotizability and imagery modality preference: Do highs and lows live in the same world? *Contemporary Hypnosis*. 2007; 24(2):64–75.
- Carlsson K, Petrovic P, Skare S, Petersson KM, Ingvar M. Tickling expectations: Neural processing in anticipation of a sensory stimulus. *Journal of Cognitive Neuroscience*. 2000; 12(4):691–703. [PubMed: 10936920]
- Case L, Abrams R, Ramachandran VS. Immediate interpersonal and intermanual referral of sensations following anesthetic block of one arm. *Archives of Neurology*. 2010; 67(12):1521–1523. [PubMed: 21149815]
- Case L, Gosavi R, Ramachandran VS. Heightened Sensory and Motor Referral Induced by Nerve Block or Topical Anesthetic. *Neuropsychologia*. 2013; 51(10):1823–1828. [PubMed: 23791606]
- Chan BL, Witt R, Charrow AP, Magee A, Howard R, Pasquina PF, Heilman KM, Tsao JW. Mirror therapy for phantom limb pain. *New England Journal of Medicine*. 2007; 357(21):2206–2207. [PubMed: 18032777]
- Cheng Y, Lin CP, Liu HL, Hsu YY, Lim KE, Hung D, Decety J. Expertise modulates the perception of pain in others. *Current Biology*. 2007; 17(19):1708–1713. [PubMed: 17900903]
- Chong TT-J, Cunnington R, Williams MA, Kanwisher N, Mattingley JB. fMRI adaptation reveals mirror neurons in human inferior parietal cortex. *Current Biology*. 2008; 18(20):1576–1580. [PubMed: 18948009]
- Cochin S, Barthelemy C, Roux S, Martineau J. Observation and execution of movement: Similarities demonstrated by quantified electroencephalography. *European Journal of Neuroscience*. 1999; 11:1839–1842. [PubMed: 10215938]
- Coslett HB, Medina J, Klot D, Burkey AR. Mental motor imagery indexes pain: the hand laterality task. *European Journal of Pain*. 2010; 14(10):1007–1013. [PubMed: 20638306]
- Craigheo L, Bello A, Fadiga L, Rizzolatti G. Hand action preparation influences the responses to hand pictures. *Neuropsychologia*. 2002; 40:492–502. [PubMed: 11749979]



- Craver-Lemley C, Reeves A. How visual imagery interferes with vision. *Psychological Review*. 1992; 99:633–649. [PubMed: 1454902]
- Cross KA, Iacoboni M. To imitate or not: Avoiding imitation involves preparatory inhibition of motor resonance. *NeuroImage*. 2014; 91:118–236.
- Damasio A, Meyer K. Behind the looking-glass. *Nature*. 2008; 454:167–168. [PubMed: 18615070]
- Decety J. The neurophysiological basis of motor imagery. *Behavioral Brain Research*. 1996; 77:45–52.
- Decety J, Grèzes J. The power of simulation: Imagining one's own and other's behavior. *Brain Research Res*. 2006; 1079(1):4–14.
- Decety J, Perani D, Jeannerod M, Bettinardi V, Tadary B, Woods R, Mazziotta JC, Fazio F. Mapping motor representations with PET. *Nature*. 1994; 371:600–602. [PubMed: 7935791]
- Decety J, Michalska KJ, Akitsuki Y. Who caused the pain? An fMRI investigation of empathy and intentionality in children. *Neuropsychologia*. 2008; 46(11):2607–2614. [PubMed: 18573266]
- Deiber M-P, Ibanez V, Honda M, Sadato N, Raman R, Hallett M. Cerebral processes related to visuomotor imagery and generation of simple finger movements studied with positron emission tomography. *NeuroImage*. 1998; 7(2):73–85. [PubMed: 9571132]
- Derbyshire SW, Whalley MG, Stenger VA, Oakley DA. Cerebral activation during hypnotically induced and imagined pain. *NeuroImage*. 2004; 32(1):392–401. [PubMed: 15325387]
- Devue C, Collette F, Baeteau E, Degueldre C, Luxen A, Maquet P, Brédart S. Here I am: the cortical correlates of visual self-recognition. *Brain Res*. 2007; 1143:169–82. [PubMed: 17306235]
- de Vignemont F. Shared body representations and the “Whose” system. *Neuropsychologia*. 2014; 55:128–136. [PubMed: 23988295]
- Diers M, Christmann C, Koeppel C, Ruf M, Flor H. Mirrored, imagined and executed movements differentially activate sensorimotor cortex in amputees with and without phantom limb pain. *PAIN*. 2010; 149(2):296–304. [PubMed: 20359825]
- Dickstein R, Deutsch JE. Motor imagery in physical therapist practice. *Physical therapy*. 2007; 87(7): 942–953. [PubMed: 17472948]
- Dinstein I, Hasson U, Rubin N, Heeger DJ. Brain areas selective for both observed and executed movements. *Journal of Neurophysiology*. 2007; 98:1415–1427. [PubMed: 17596409]
- Driver J, Spence C. Multisensory perception: Beyond modularity and convergence. *Current Biology*. 2000; 10(20):R731–R735. [PubMed: 11069095]
- Ebisch SJ, Perrucci MG, Ferretti A, Del Gratta C, Romani GL, Gallese V. The sense of touch: embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *Journal of Cognitive Neuroscience*. 2008; 20:1611–1623. [PubMed: 18345991]
- Egnera T, Jamieson G, Gruzelier J. Hypnosis decouples cognitive control from conflict monitoring processes of the frontal lobe. *NeuroImage*. 2005; 27(4):969–978. [PubMed: 15964211]
- Ehrsson HH, Geyer S, Naito E. Imagery of voluntary movement of fingers, toes, and tongue activates corresponding body-part-specific motor representations. *Journal of Neurophysiology*. 2003; 90:3304–3316.
- Ersland L, Rosen G, Lundervold A, Smievoll AI, Tillung T, Sundberg H, Hugdahl K. Phantom limb “fingertapping” causes primary motor cortex activation: An fMRI study. *Neuroreport*. 1996; 8:207–210. [PubMed: 9051782]
- Fadiga L, Fogassi L, Pavesi G, Rizzolatti G. Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*. 1995; 73(6):2608–2611. [PubMed: 7666169]
- Filimon F, Nelson JD, Hagler DJ, Sereno MI. Human cortical representations for reaching: Mirror neurons for execution, observation, and imagery. *NeuroImage*. 2007; 37(4):1315–1328. [PubMed: 17689268]
- Fink GR, Marshall JC, Weiss PH, Stephan T, Grefkes C, Shah NJ, Zilles K, Dieterich M. Performing allocentric visuospatial judgments with induced distortion of the egocentric reference frame: an fMRI study with clinical implications. *Neuroimage*. 2003; 20:1505–1517. [PubMed: 14642463]
- Fiorio M, Haggard P. Viewing the body prepares the brain for touch: effects of TMS over somatosensory cortex. *European Journal of Neuroscience*. 2005; 22:773–777. [PubMed: 16101759]

- Filimon F, Nelson JD, Hagler DJ, Sereno MI. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage*. 2007; 37(4):1315–1328. [PubMed: 17689268]
- Fisher JP, Hassan DT, O'Connor N. *Minerva*. British Medical Journal. 1995; 310:70.
- Fitzgibbon BM, Giummarra MJ, Georgiou-Karistianis N, Enticott PG, Bradshaw JL. Shared pain: from empathy to synaesthesia. *Neurosci. Biobehav. Rev.* 2010; 34:500–512. [PubMed: 19857517]
- Fitzgibbon BM, Enticott PG, Rich AN, Giummarra MJ, Georgiou-Karistianis N, Bradshaw JL. Mirror-sensory synaesthesia: exploring 'shared' sensory experiences as synaesthesia. *Neurosci Biobehav Rev.* 2012; 36(1):645–57. [PubMed: 21986634]
- Foley MA, Johnson MK. Confusions between memories for performed and imagined actions: a developmental comparison. *Child Development*. 1985; 65(5):1145–1155. [PubMed: 4053736]
- Fourkas AD, Avenanti A, Urgesi C, Aglioti S. Corticospinal facilitation during first and third person imagery. *Experimental Brain Research*. 2006; 168(1-2):143–151. [PubMed: 16044298]
- Gallese V, Goldman A. Mirror neurons and the simulation theory of mind reading. *Trends in Cognitive Sciences*. 1998; 12:493–501. [PubMed: 21227300]
- Gallese V, Fadiga L, Fogassi L, Rizzolatti G. Action recognition in the premotor cortex. *Brain*. 1996; 119:593–609. [PubMed: 8800951]
- Ganis G, Keenan JP, Kosslyn SM, Pascual-Leone A. Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex*. 2000; 10:175–180. [PubMed: 10667985]
- Gazzola V, Spezio ML, Etzel JA, Castelli F, Adolphs R, Keysers C. Primary somatosensory cortex discriminates affective significance in social touch. *Proc Natl Acad Sci U S A*. 2012; 109(25):E1657–1666. [PubMed: 22665808]
- Gentili ME, Verton C, Kinirons B, Bonnet F. Clinical perception of phantom limb sensation in patients with brachial plexus block. *European Journal of Anaesthesiology*. 2002; 19:105–108. [PubMed: 11999591]
- Gerardin E, Sirigu A, Lehericy S, Poline J-B, Gaymard B, Marsault C, Agid Y, Le Bihan D. Partially overlapping neural networks for real and imagined hand movements. *Cerebral Cortex*. 2010; 10(11):1093–1104. [PubMed: 11053230]
- Gilbert DT, Gill MJ, Wilson TD. The future is now: Temporal correction in affective forecasting. *Organizational Behavior and Human Decision Processes*. 2002; 88(1):430–444.
- Goller AI, Richards K, Novak S, Ward J. Mirror-touch synaesthesia in the phantom limbs of amputees. *Cortex*. 2013; 49(1):243–51. [PubMed: 22981809]
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G. Localization of grasp representations in humans by positron emission tomography. *Experimental Brain Research*. 1996; 112(1):103–111. [PubMed: 8951412]
- Grèzes J, Decety J. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Human Brain Mapping*. 2001; 12(1):1–19. [PubMed: 11198101]
- Haggard P, Christakou A, Serino A. Viewing the body modulates tactile receptive fields. *Experimental Brain Research*. 2007; 180:187–193. [PubMed: 17508208]
- Hall C, Bernoties L, Schmidt D. Motor imagery can cause motor interference and facilitation effects: Interference effects of mental imagery on a motor task. *British Journal of Psychology*. 1995; 86(2): 181–190. [PubMed: 7795940]
- Hargadon R, Bowers KS, Woody EZ. Does counterpain imagery mediate hypnotic analgesia? *Journal of Abnormal Psychology*. 1995; 104(3):508–516. [PubMed: 7673574]
- Hari R, Bourguignon M, Piitulainen H, Smeds E, De Tiège X, Jousmäki V. Human primary motor cortex is both activated and stabilized during observation of other person's phasic motor actions. *Phil. Trans. R. Soc. B*. 2014; 369:20130171. [PubMed: 24778370]
- Harris IM, Miniussi C. Parietal lobe contribution to mental rotation demonstrated with rTMS. *Journal of Cognitive Neuroscience*. 2003; 15(3):315–323. [PubMed: 12729485]
- Hennenlotter A, Dresel C, Castrop F, Ceballos-Baumann AO, Wohlschläger AM, Haslinger B. The link between facial feedback and neural activity within central circuitries of emotion—New insights from Botulinum toxin–induced denervation of frown muscles. *Cerebral Cortex*. 2009; 19(3):537–542. [PubMed: 18562330]

- Hlushchuk Y, Hari R. Transient suppression of ipsilateral primary somatosensory cortex during tactile finger stimulation. *Journal of Neuroscience*. 2006; 26:5819–5824. [PubMed: 16723540]
- Holle H, Banissy MJ, Wright T, Bowling N, Ward J. “That’s not a real body”: Identifying stimulus qualities that modulate synaesthetic experiences of touch. *Consciousness and Cognition*. 2011; 20(3):720–726. [PubMed: 21237676]
- Holle H, Warne K, Seth AK, Critchley HD, Ward J. Neural basis of contagious itch and why some people are more prone to it. *Proceedings of the National Academy of Science*. 2012; 109(48): 19816–19821.
- Hugdahl K, Rosen G, Erslund L, Lundervold A, Smievoll AI, Barndon R, Thomsen T. Common pathways in mental imagery and pain perception: an fMRI study of a subject with an amputated arm. *Scandinavian Journal of Psychology*. 2001; 42:269–275. [PubMed: 11501740]
- Iacoboni M. Imitation, Empathy, and Mirror Neurons. *Annual Review of Psychology*. 2009; 60:653–670.
- Ionta S, Fourkas AD, Fiorio M, Aglioti SM. The influence of hands posture on mental rotation of hands and feet. *Experimental Brain Research*. 2007; 183(1):1–7. [PubMed: 17643238]
- Jackson JH. *Selected Writings*. Hodder and Stoughton. 1932
- Jacobs A, Shiffrar M. Walking perception by walking observers. *Journal of Experimental Psychology: Human Perception and Performance*. 2005; 31(1):157–169. [PubMed: 15709870]
- Jeannerod M. The representing brain: Neural correlates of motor imagery and intention. *Behavioral and Brain Sciences*. 1994; 17:187–245.
- Jeannerod M, Frak VG. Mental imaging of motor activity in humans. *Current Opinion in Neurobiology*. 1999; 9:735–739. [PubMed: 10607647]
- Johnson MH, Breakwell G, Douglas W, Humphries S. The effects of imagery and sensory detection distractors on different measures of pain: How does distraction work? *British Journal of Clinical Psychology*. 1998; 37(2):141–154. [PubMed: 9631203]
- Johnson SH, Sprehn G, Saykin AJ. Intact motor imagery in chronic upper limb hemiplegics: Evidence for activity-independent action representations. *Journal of Cognitive Neuroscience*. 2002; 14(6): 841–852. [PubMed: 12191452]
- Johnson-Frey SH. Stimulation through simulation? Motor imagery and functional reorganization in hemiplegic stroke patients. *Brain and Cognition*. 2004; 55(2):328–331. [PubMed: 15177807]
- Kaplan JT, Meyer K. Multivariate pattern analysis reveals common neural patterns across individuals during touch observation. *NeuroImage*. 2012; 60(1):204–212. [PubMed: 22227887]
- Kennett S, Taylor-Clarke M, Haggard P. Noninformative vision improves the spatial resolution of touch in humans. *Current Biology*. 2001; 11:1188–1191. [PubMed: 11516950]
- Keysers C, Gazzola V. Unifying social cognition. *Contemporary Neuroscience*. 2009; 1:1–35.
- Keysers C, Kaas JH, Gazzola V. Somatosensation in social perception. *Nature Reviews Neuroscience*. 2010; 11:417–428. [PubMed: 20445542]
- Keysers C, Wicker B, Gazzola V, Jean-Luc A, Fogassi L, Gallese V. A Touching Sight: SII/PV Activation during the Observation and Experience of Touch. *Neuron*. 2004; 42(2):335–346. [PubMed: 15091347]
- Kilner JM, Paulignan Y, Blakemore SJ. An interference effect of observed biological movement on action. *Current Biology*. 2003; 13:522–525. [PubMed: 12646137]
- Knight RT, Staines WR, Swick D, Chao LL. Prefrontal cortex regulates inhibition and excitation in distributed neural networks. *Acta Psychologica*. 1999; 101(2-3):159–178. [PubMed: 10344184]
- Kogon MM, Jasiukaitis P, Berardi A, Gupta M, Kosslyn SM, Spiegel D. Imagery and hypnotizability revisited. *International Journal of Clinical and Experimental Hypnosis*. 1998; 46(4):363–370. [PubMed: 9780527]
- Kojo I. The effects of mental imagery on skin temperature and skin temperature sensation. *Scandinavian Journal of Psychology*. 1985; 26(1):314–320. [PubMed: 4089560]
- Ku J, Kim J-J, Jung YC, Park IH, Lee H, Han K, Yoon KJ, Kim IY, Kim SI. Brain mechanisms involved in processing unreal perceptions. *NeuroImage*. 2008; 43(4):793–800. [PubMed: 18801444]

- Kuehn E, Trampel R, Mueller K, Turner R, Schütz-Bosbach S. Judging roughness by sight—A 7-tesla fMRI study on responsivity of the primary somatosensory cortex during observed touch of self and others. *Human brain mapping*. 2013; 34(8):1882–1895. [PubMed: 22422484]
- Langner R, Kellermann T, Boers F, Sturm W, Willmes K, Eickhoff SB. Modality-Specific Perceptual Expectations Selectively Modulate Baseline Activity in Auditory, Somatosensory, and Visual Cortices. *Cerebral Cortex*. 2011
- Li S. Movement-specific enhancement of corticospinal excitability at subthreshold levels during motor imagery. *Experimental Brain Research*. 2007; 179(3):517–524.
- Liepert J, Neveling N. Motor excitability during imagination and observation of foot dorsiflexions. *Journal of Neural Transmission*. 2009; 116(12):1613–1619.
- Lingnau A, Gesierich B, Caramazza A. Asymmetric fMRI adaptation reveals no evidence for mirror neurons in humans. *PNAS*. 2009; 106(24):9925–9930. [PubMed: 19497880]
- Lorey B, Naumann T, Pilgramm S, Petermann C, Bischoff M, Zentgraf K, Stark R, Vaitl D, Munzert J. How equivalent are the action execution, imagery, and observation of intransitive movements? Revisiting the concept of somatotopy during action simulation. *Brain and Cognition*. 2013; 81:139–150. [PubMed: 23207575]
- Lotze M, Montoya P, Erb M, Hulsmann E, Flor H, Klose U, Birbaumer N, Grodd W. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: An fMRI study. *Journal of Cognitive Neuroscience*. 1999; 11:491–501. [PubMed: 10511638]
- Lotze M, Flor H, Grodd W, Larbig W, Birbaumer N. Phantom movements and pain: An fMRI study in upper limb amputees. *Brain*. 2001; 124(11):2268–2277. [PubMed: 11673327]
- Lakin JL, Chartrand TL. Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological science*. 2003; 14(4):334–339. [PubMed: 12807406]
- Maeda F, Kleiner-Fisman G, Pascual-Leone A. Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. *Journal of Neurophysiology*. 2002; 87:1329–1335. [PubMed: 11877507]
- Maister L, Banissy MJ, Tsakiris M. Mirror-touch synaesthesia changes representations of self-identity. *Neuropsychologia*. 2013; 51:802–808. [PubMed: 23391559]
- Maravita A, Spence C, Sergent C, Driver J. Seeing your own touched hands in a mirror modulates cross-modal interactions. *Psychological Science*. 2002; 13:350–355. [PubMed: 12137138]
- Marsh KL, Richardson MJ, Schmidt RC. Social connection through joint action and interpersonal coordination. *Topics in Cognitive Science*. 2009; 1(2):320–339. [PubMed: 25164936]
- Maslach C, Marshall G, Zimbardo PG. Hypnotic Control of Peripheral Skin Temperature: A Case Report. *Psychophysiology*. 1972; 9(6):600–605. [PubMed: 5076027]
- Miall RC, Stanley J, Todhunter S, Levick C, Lindo S, Miall JD. Performing hand actions assists the visual discrimination of similar hand postures. *Neuropsychologia*. 2006; 44:966–976. [PubMed: 16249009]
- Morse JM, Mitcham C. Compathy: the contagion of physical distress. *Journal of Advanced Nursing*. 1997; 26(4):649–657. [PubMed: 9354974]
- Möttönen R, Järveläinen J, Sams M, Hari R. Viewing speech modulates activity in the left SI mouth cortex. *NeuroImage*. 2005; 24(3):731–737. [PubMed: 15652308]
- Mukamel R, Ekstrom AD, Kaplan J, Jacoboni M, Fried I. Single-neuron responses in humans during execution and observation of actions. *Current Biology*. 2010; 20(8):750–756. [PubMed: 20381353]
- Mulder T, Zijlstra S, Zijlstra W, Hochstenbach J. The role of motor imagery in learning a totally novel movement. *Experimental Brain Research*. 2004; 154(2):211–217. [PubMed: 14508635]
- Musalek M, Podreka I, Walter H, Suess E, Passweg V, Nutzinger D, Strobl R, Lesch OM. Regional brain function in hallucinations: A study of regional cerebral blood flow with 99m-Tc-HMPAO-SPECT in patients with auditory hallucinations, tactile hallucinations, and normal controls. *Comprehensive Psychiatry*. 1989; 30(1):99–108. [PubMed: 2784369]
- Muthukumaraswamy SD, Singh KD. Modulation of the human mirror neuron system during cognitive activity. *Psychophysiology*. 2008; 45(6):896–905. [PubMed: 18823416]

- Neal DT, Chartrand TL. Embodied emotion perception amplifying and dampening facial feedback modulates emotion perception accuracy. *Social Psychological and Personality Science*. 2011; 2(6):673–678.
- Nemoto K, Mizukami K, Hori T, Tachikawa H, Ota M, Takeda T, Ohnishi T, Matsuda H, Asada T. Hyperperfusion in primary somatosensory region related to somatic hallucination in the elderly. *Psychiatry and Clinical Neurosciences*. 2010; 64(4):421–425. [PubMed: 20492558]
- Nico D, Daprati E, Rigal E, Parsons L, Sirigu A. Left and right hand recognition in upper limb amputees. *Brain*. 2004; 127(1):120–132. [PubMed: 14607796]
- Niemeier V, Gieler U. Observations during itch-inducing lecture. *Dermatology and Psychosomatics*. 2000; 1(Suppl 1):15–18.
- Nisbett RE, Kanouse DE. Obesity, food deprivation, and supermarket shopping behavior. *Journal of Personality and Social Psychology*. 1969; 12:289–294. [PubMed: 5821855]
- Oberman LM, McCleery JP, Ramachandran VS, Pineda JA. EEG evidence for mirror neuron activity during the observation of human and robot actions: Toward an analysis of the human qualities of interactive robots. *Neurocomputing*. 2007a; 70(13-15):2194–2203.
- Oberman LM, Winkielman P, Ramachandran VS. Face to face: Blocking facial mimicry can selectively impair recognition of emotional expressions. *Social Neuroscience*. 2007b; 2(3&4): 167–178. [PubMed: 18633815]
- Obhi SS, Hogeveen J. The controlled imitation task: a new paradigm for studying self-other control. *PeerJ*. 2013; 1:e161. [PubMed: 24109546]
- Oh DW, Kim JS, Kim SY, Yoo EY, Jeon HS. Effect of motor imagery training on symmetrical use of knee extensors during sit-to-stand and stand-to-sit tasks in post-stroke hemiparesis. *Neurorehabilitation*. 2010; 26(4):307–315. [PubMed: 20555153]
- Ondobaka S, de Lange FP, Newman-Norlund RD, Wiemers M, Bekkering H. Interplay Between Action and Movement Intentions During Social Interaction. *Psychological Science*. 2012; 23(1): 30–35. [PubMed: 22157675]
- Oosterhof NN, Tipper SP, Downing PE. Visuo-motor imagery of specific manual actions: A multivariate pattern analysis fMRI study. *Neuroimage*. 2012; 63(1):262–271. [PubMed: 22766163]
- Page SJ, Szaflarski JP, Eliassen JC, Pan H, Cramer SC. Cortical plasticity following motor skill learning during mental practice in stroke. *Neurorehabilitation and Neural Repair*. 2009a; 23(4): 382–388. [PubMed: 19155350]
- Paoletti G, Varanini M, Balocchi R, Morizzo C, Palombo C, Santarcangelo EL. Cardiovascular and respiratory correlates of deep nociceptive stimulation, suggestions for analgesia, pain imagery and cognitive load as a function of hypnotizability. *Brain Research Bulletin*. 2010; 82(1-2):65–73. [PubMed: 20227467]
- Papoiu ADP, Wang H, Coghill RC, Chan YH, Yosipovitch G. Contagious itch in humans: A study of visual “transmission” of itch in atopic dermatitis and healthy subjects. *British Journal of Dermatology*. 2011; 164(6):1299–1303. [PubMed: 21410682]
- Parsons LM. Imagined spatial transformations of one's body. *Journal of Experimental Psychology: General*. 1987; 116:172–191. [PubMed: 2955072]
- Parsons LM. Temporal and kinematic properties of motor behavior reflected in mentally simulated action. *Journal of Experimental Psychology: Human Perception and Performance*. 1994; 20:709–730. [PubMed: 8083630]
- Perky CW. An experimental study of imagination. *American Journal of Psychology*. 1910; 21:422–452.
- Petit LS, Pegna AJ, Mayer E, Hauert C-A. Representation of anatomical constraints in motor imagery: Mental rotation of a body segment. *Brain and Cognition*. 2003; 51(1):95–101. [PubMed: 12633591]
- Pfister R, Heinemann A, Kiesel A, Thomaschke R, Janczyk M. Do Endogenous and Exogenous Action Control Compete for Perception? *Journal of Experimental Psychology: Human Perception and Performance*. 2012; 38(2):279–284. [PubMed: 22201462]
- Porro CA, Facchin P, Fusi S, Dri G, Fadiga L. Enhancement of force after action observation: Behavioral and neurophysiological studies. *Neuropsychologia*. 2007; 45(13):3114–3121. [PubMed: 17681358]



- Porro CA, Francescato MP, Cettolo V, Diamond ME, Baraldi P, Bazzochi M, Di Prampero PE. Primary motor and sensory cortex activation during motor performance and motor imagery: A functional magnetic resonance study. *Journal of Neuroscience*. 1996; 16:7688–7698. [PubMed: 8922425]
- Posner MI, Peterson SE. The attention system of the human brain. *Annual Review of Neuroscience*. 1990; 13:25–42.
- Raij T, Numminen J, Narvanen S, Hiltunen J, Hari R. Strength of prefrontal activation predicts intensity of suggestion-induced pain. *Human Brain Mapping*. 2009; 30(9):2890–2897. [PubMed: 19184995]
- Raffin E, Mattout J, Reilly KT, Giraux P. Disentangling motor execution from motor imagery with the phantom limb. *Brain*. 2012; 135(Pt 2):582–95. [PubMed: 22345089]
- Ramachandran VS, Hirstein W. The perception of phantom limbs: The D.O. Hebb lecture. *Brain*. 1998; 121:1603–1630. [PubMed: 9762952]
- Ramachandran VS, Brang D. Sensations evoked in patients with amputation from watching an individual whose corresponding intact limb is being touched. *Archives of Neurology*. 2009; 66(10):1281–1284. [PubMed: 19822785]
- Ramachandran VS, Rogers-Ramachandran D. Synaesthesia in phantom limbs induced with mirrors. *Proceedings: Biological Sciences*. 1996; 263(1369):377–386.
- Ramachandran VS, Rogers-Ramachandran D, Cobb S. Touching the phantom limb. *Nature*. 1995; 377:489–90. [PubMed: 7566144]
- Ramenzonei VC, Riley MA, Shockley K, Davis T. Carrying the height of the world on your ankles: Encumbering observers reduces estimates of how high an actor can jump. *The Quarterly Journal of Experimental Psychology*. 2008; 61(10):1487–1495. [PubMed: 18609383]
- Rauch SL, Savage CR, Alpert NM, Miguel EC, Baer L, Breiter HC, Fischman AJ, Manzo PA, Moretti C, Jenike MA. A positron emission tomographic study of simple phobic symptom provocation. *Archives of General Psychiatry*. 1995; 52(1):20–28. [PubMed: 7811159]
- Reed CL, Farah MJ. The psychological reality of the body schema: a test with normal participants. *Journal of Experimental Psychology: Human Perception and Performance*. 1995; 21(2):334–343. [PubMed: 7714475]
- Richardson, A. *Mental Imagery*. Springer Berlin Heidelberg; 1969. *Memory Imagery*.; p. 43-92.
- Rie anský I, Paul N, Kölbl S, Stieger S, Lamm C. Beta oscillations reveal ethnicity ingroup bias in sensorimotor resonance to pain of others. *Social cognitive and affective neuroscience*. 2014:nsu139.
- Rizzolatti G, Fogassi L, Gallese V. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci*. 2001; 2:661–670. [PubMed: 11533734]
- Rizzolatti G, Fogassi L. The mirror mechanisms: recent findings and perspectives. *Philos Trans R Soc Lond B Biol Sci*. 2014; 369(1644):20130420. [PubMed: 24778385]
- Rizzolatti G, Fabbri-Destro M, Cattaneo L. Mirror neurons and their clinical relevance. *Nature Clinical Practice Neurology*. 2009; 5:24–34.
- Rockland K, Ojima H. Multisensory convergence in calcarine visual areas in macaque monkey. *International Journal of Psychophysiology*. 2003; 50(1-2):19–26. [PubMed: 14511833]
- Rorden C, Heutink J, Greenfield E, Robertson IH. When a rubber hand ‘feels’ what the real hand cannot. *Neuroreport*. 1999; 10(1):135–138. [PubMed: 10094149]
- Roth M, Decety J, Raybaud M, Massarelli R, Delon-Martin C, Segebarth C, Morand S, Gemignani A, Decors M, Jeannerod M. Possible involvement of primary motor cortex in mentally simulated movement: a fMRI study. *NeuroReport*. 1996; 7:1280–1284. [PubMed: 8817549]
- Santarcangelo EL, Cavallaro E, Mazzoleni S, Marano E, Ghelarducci B, Dario P, Micera S, Sebastiani L. Kinematic strategies of upper limbs lowering during suggestions of heaviness: a real-simulator design. *Experimental Brain Research*. 2005; 162:35–45. [PubMed: 15502975]
- Sathian K. Intermanual referral of sensation to anesthetic hands. *Neurology*. 2000; 54(9):1866–1868. [PubMed: 10802803]
- Schaefer M, Heinze H-J, Rotte M. Viewing touch improves tactile sensory threshold. *NeuroReport*. 2005; 16:367–370. [PubMed: 15729139]



- Schaefer M, Flor H, Heinze H-J, Rotte M. Dynamic modulation of the primary somatosensory cortex during seeing and feeling a touched hand. *NeuroImage*. 2006; 29(2):587–592. [PubMed: 16099177]
- Schmalzl L, Ragnö C, Ehrsson HH. An Alternative to Traditional Mirror Therapy: Illusory Touch Can Reduce Phantom Pain When Illusory Movement Does Not. *Clinical Journal of Pain*. 2013; 29(10) doi: 10.1097/AJP.0b013e3182850573.
- Schütz-Bosbach S, Prinz W. Perceptual resonance: action-induced modulation of perception. *Trends in Cognitive Sciences*. 2007; 11(8):349–355. [PubMed: 17629544]
- Schweiger A, Parducci A. Nocebo: The psychologic induction of pain. *Pavlovian Journal of Biological Science*. 1981; 16:140–143. [PubMed: 7290754]
- Schwoebel J, Boronat BC, Coslett HB. The man who executed “imagined” movements: Evidence for dissociable components of the body schema. *Brain and Cognition*. 2002; 50:1–16. [PubMed: 12372347]
- Segal SJ, Fusella V. Influence of imaged pictures and sounds on detection of visual and auditory signals. *Journal of Experimental Psychology*. 1970; 83(3:1):458–464. [PubMed: 5480913]
- Shepard RN, Metzler J. Mental rotation of three dimensional objects. *Science*. 1971; 171:701–703. [PubMed: 5540314]
- Shergill SS, Cameron LA, Brammer MJ, Williams SC, Murray RM, McGuire PK. Modality specific correlates of auditory and somatic hallucinations. *Journal of Neurology, Neurosurgery and Psychiatry*. 2001; 71:688–690.
- Silva S, Loubinoux I, Olivier M, Bataille B, Fourcade O, Samii K, Jeannerod M, Démonet J-F. Impaired visual hand recognition in preoperative patients during Brachial Plexus anesthesia: Importance of peripheral neural input for mental representation of the hand. *Anesthesiology*. 2011; 114(1):126–134. [PubMed: 21169795]
- Sinigaglia C. What type, if any, of action understanding is subserved by mirror neurons? *Neuroscience Letters*. 2013; 540:59–61. [PubMed: 23089283]
- Schneider, KG.; Hempel, RJ.; Lynch, TR. That “poker face” just might lose you the game!. The impact of expressive suppression and mimicry on sensitivity to facial expressions of emotion. 2013.
- Sobhani M, Fox GR, Kaplan J, Aziz-Zadeh L. Interpersonal liking modulates motor-related neural regions. *PLOS One*. 2012; 7(10):e46809. [PubMed: 23071644]
- Stephan KM, Fink GR, Passingham D, Silbersweig D, Ceballos-Baumann AO, Frith CD, Frackowiack RSJ. Functional anatomy of the mental representation of upper extremity movements in healthy subjects. *Journal of Neurophysiology*. 1995; 73:373–386. [PubMed: 7714579]
- Strafella A, Paus T. Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *Neuroreport*. 2000; 11(10):2289–2292. [PubMed: 10923687]
- Takasugi J, Matsuzawa D, Murayama T, Nakazawa K, Numata K, Simizu E. Referred sensations induced by a mirror box in healthy subjects. *Psychological Research*. 2011; 75:54–60. [PubMed: 20505951]
- Tamir R, Dickstein R, Huberman M. Integration of motor imagery and physical practice in group treatment applied to subjects with Parkinson's Disease. *Neurorehabilitation and Neural Repair*. 2007; 21(1):68–75. [PubMed: 17172556]
- Thomas R, Press C, Haggard P. Shared representations in body perception. *Acta Psychologica*. 2006; 121:317–330. [PubMed: 16194527]
- Tia B, Saimpont A, Paizis C, Mourey F, Fadiga L, Pozzo T. Does observation of postural imbalance induce a postural reaction? *PLoS ONE*. 2011; 6(3):e17799. [PubMed: 21423622]
- Tipper SP, Lloyd D, Shorland B, Dancer C, Howard L, McGlone F. Vision influences tactile perception without proprioceptive orienting. *Neuroreport*. 1998; 9:1741–1744. [PubMed: 9665593]
- Tsakiris M, Hesse MD, Boy C, Haggard P, Fink GR. Neural signatures of body-ownership: A sensory network for bodily self-consciousness. *Cerebral Cortex*. 2007; 17:2235–2244. [PubMed: 17138596]
- Turner AC, McIntosh DN, Moody EJ. Don't Listen With Your Mouth Full: The Role of Facial Motor Action in Visual Speech Perception. *Language and Speech*. 2014 0023830914542305.

- Ushioda T, Watanabe Y, Sanjo Y, Yamane GY, Abe S, Tsuji Y, et al. Visual and auditory stimuli associated with swallowing activate mirror neurons: a magnetoencephalography study. *Dysphagia*. 2012; 27:504–513. [PubMed: 22395851]
- Van Ede F, Jensen O, Maris E. Tactile expectation modulates pre-stimulus  $\beta$ -band oscillations in human sensorimotor cortex. *NeuroImage*. 2010; 51(2):867–876. [PubMed: 20188186]
- Van Tilburg MAL, Chitkara DK, Palsson OS, Turner M, Blois-Martin N, Ulshen M, Whitehead WE. Audio-recorded guided imagery treatment reduces functional abdominal pain in children: A pilot study (2009). *Pediatrics*. 2009; 124(5):e890–e897. [PubMed: 19822590]
- Wagstaff GF, Cole JC, Brunas-Wagstaff J. Effects of hypnotic induction and hypnotic depth on phonemic fluency: A test of the frontal inhibition account of hypnosis. *International Journal of Psychology and Psychological Therapy*. 2007; 7(1):27–40.
- Weeks SR, Tsao JW. Incorporation of another person's limb into body image relieves phantom limb pain: A case study. *Neurocase: The Neural Basis of Cognition*. 2010; 16(6):461–465.
- Whipple B, Ogden G, Komisaruk BR. Physiological correlates of imagery-induced orgasm in women. *Archives of Sexual Behavior*. 1992; 21:121–133. [PubMed: 1580785]
- Wolpert DM. Computational approaches to motor control. *Trends in Cognitive Science*. 1997; 1:209–216.
- Wolpert DM, Miall RC. Forward models for physiological motor control. *Neural Networks*. 1996; 9(8):1265–1279. [PubMed: 12662535]
- Wohlschläger A. Visual motion priming by invisible actions. *Vision Research*. 2000; 40:925–930. [PubMed: 10720663]
- Yamaguchi S, Yamagata S, Bokura H, Toyoda G, Nagai A, Takahashi K, Kobayashi S. Somatosensory disinhibition and frontal alien hand signs following medial frontal damage. *Journal of Clinical Neuroscience*. 2006; 13:279–282. [PubMed: 16439131]
- Yoo SS, Freeman DK, McCarthy JJ III, Jolesz FA. Neural substrates of tactile imagery: a functional MRI study. *Neuroreport*. 2003; 14(4):581–585. [PubMed: 12657890]
- Zimmermann-Schlatter A, Schuster C, Puhan MA, Siekierka E, Steurer J. Efficacy of motor imagery in post-stroke rehabilitation: a systematic review. *Journal of Neuroengineering and Rehabilitation*. 2008; 5(1)

### Highlights

- Motor imagery, observed action, and motor production show strong neural overlap
- Somatosensory imagery, observed touch, and somatosensation also show overlap
- Simulation (imagery and observation), perception, and action influence one another
- Numerous brain areas regulate influence of simulation on action and perception
- Deafferentation and brain injury demonstrate dynamic regulation of simulation