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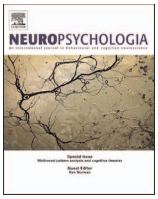

Common coding and dynamic interactions between observed, imagined, and experienced motor and somatosensory activity

Q1 Laura K. Case [a,b,*,1], Jaime Pineda [c], Vilayanur S. Ramachandran [a]

[a] Center for Brain and Cognition, University of California, San Diego, USA
Q3 [b] Pain and Integrative Neuroscience Branch, National Center for Complementary and Integrative Health, National Institutes of Health, Bethesda, MD, USA
[c] Department of Cognitive Science, University of California, San Diego, USA

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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.

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[*] Corresponding author at: National Center for Complementary and Integrative Health, National Institutes of Health, Bethesda, Maryland, USA. Fax: +1 301 480 5678.
E-mail address: laura.case@nih.gov (L.K. Case).
[1] Current mailing address: BG 10-CRC RM 4-1730 Mail Stop 1302, 10 Center Dr, Bethesda, MD 20814, USA.

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1. 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 and 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 and Mattingley, 2001; Fitzgibbon BM1 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 and 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 and 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 and 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 “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 are 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.

2. The motor system

2.1. Motor referral

2.1.1 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 and Decety, 2001; Rizzolatti et al., 2001). We use the term ‘motor referral’ to describe this covert, spontaneous mirroring of others.[2] 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 et al., 1999; Muthukumaraswamy and Singh, 2008; Keysers and Gazzola, 2009; Ushioda et al., 2012). Individual subjects consistently activate shared voxels during functional magnetic resonance imaging (fMRI) of observed and

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[2] 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).

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