

## Building a motor simulation de novo: Observation of dance by dancers

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**Research on action simulation identifies brain areas that are active while imagining or performing simple overlearned actions. Are areas engaged during imagined movement sensitive to the amount of actual physical practice? In the present study, participants were expert dancers who learned and rehearsed novel, complex whole-body dance sequences 5 h a week across 5 weeks. Brain activity was recorded weekly by fMRI as dancers observed and imagined performing different movement sequences. Half these sequences were rehearsed and half were unpracticed control movements. After each trial, participants rated how well they could perform the movement. We hypothesized that activity in premotor areas would increase as participants observed and simulated movements that they had learnt outside the scanner. Dancers' ratings of their ability to perform rehearsed sequences, but not the control sequences, increased with training. When dancers observed and simulated another dancer's movements, brain regions classically associated with both action simulation and action observation were active, including inferior parietal lobule, cingulate and supplementary motor areas, ventral premotor cortex, superior temporal sulcus and primary motor cortex. Critically, inferior parietal lobule and ventral premotor activity was modulated as a function of dancers' ratings of their own ability to perform the observed movements and their motor experience. These data demonstrate that a complex motor resonance can be built de novo over 5 weeks of rehearsal. Furthermore, activity in premotor and parietal areas during action simulation is enhanced by the ability to execute a learned action irrespective of stimulus familiarity or semantic label.**

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### Introduction

A little girl who watches *The Nutcracker* may imagine she can dance like the sugar plum fairy. Once she begins taking

dance classes and learns the movements she first saw professional dancers make, how does her cognitive representation of those movements change? It has been proposed that we understand new actions by mapping others' movements onto our own motor representations, such that there is a close correspondence between the pattern of neural activity recorded while observing, imagining and performing the same action (Rizzolatti and Craighero, 2004; Rizzolatti et al., 2001). We now investigate the extent to which this mapping system requires experience of physically performing actions in order to be engaged while observing and imagining actions.

Action simulation is defined as the internal representation of motor programs without overt movement (Jeannerod, 2001). In brain imaging experiments, imagined movement has long been used as a surrogate marker for simulation. Early positron emission tomography (PET) studies reported premotor and supplementary motor area (SMA) activation, but not primary motor cortical (M1) involvement, during imagined hand movements (Ingvar and Philipson, 1977; Roland et al., 1977, 1980a,b, 1982). Subsequent work performed with functional magnetic resonance imaging (fMRI) and PET demonstrated more detailed functional specificity within brain regions involved in simulation. Specifically, SMA is functionally divisible into subregions, including anterior rostral SMA (SMAr), which is most active during imagined movement, and posterior caudal SMA (SMAC), a subregion most active during action execution (Grafton et al., 1996; Stephan et al., 1995; Tyszka et al., 1994). Additional studies of imagined movement demonstrate involvement of ventral premotor cortex (PMv), the inferior parietal lobule (IPL), the superior temporal sulcus (STS), and, rarely, M1 (Binkofski et al., 2000; Decety, 1996; Grafton et al., 1996; Nishitani and Hari, 2000; Rizzolatti et al., 1996b; Stephan et al., 1995). Together, these five areas (SMAr, PMv, IPL, STS, and M1) are implicated as key components in an action simulation circuit.

An enduring question in the study of action simulation is whether the simulation circuit is more active for actions that are embodied, i.e., actions for which the simulator has real physical experience. This would be manifest as greater activity when an individual imagines making movements that are more physically

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familiar. The present study directly addressed this question by longitudinally comparing simulation of observed movements that participants learned to embody by daily practice to simulation of movements that participants never physically rehearsed. Critically, participants were asked to make judgments about their own ability to perform the observed movements. This self-rating measure was used as a proxy marker of action embodiment. We predicted that simulating more familiar movements would result in increased activity in the simulation circuit, along with higher ratings of ability to perform the observed movements.

One important distinction between the action simulation paradigm used in the present study and those that have been used in the past is that prior simulation studies often asked participants to simply imagine an action without external guidance. For example, subjects have been asked to imagine grasping objects with no visual stimulation (e.g., Stephan et al., 1995; Grafton et al., 1996; Binkofski et al., 2000), but the timing and detail of the imaged action were not controlled. In contrast, we asked participants to observe a dancer's actions and at the same time imagine themselves performing the actions. Thus, the visual stimulus guides and constrains the motor simulation. For clarity, we refer to our task wherein participants imagine themselves performing an observed action simply as action simulation.

Because the task used in the present study involved action observation, we must also consider how visual stimuli depicting human actions are able to drive motor regions of the brain. Evidence for an action observation/execution matching system was first discovered in the ventral premotor cortex (area F5) of monkeys using single unit recordings, and from this work emerged a new class of neurons that have both visual and motor properties, named 'mirror neurons' (Gallese et al., 1996; Rizzolatti et al., 1996a). Since this discovery, attempts to map a corresponding human mirror neuron system have compared the anatomical and functional boundaries of neural systems for action preparation, execution, observation, imitation, and simulation.

A striking and consistent result is that the motor and premotor areas that are classically associated with movement preparation are also active when simply observing the actions of others. This is demonstrated by numerous neuroimaging studies (Buccino et al., 2001; Grafton et al., 1996; Grezes and Decety, 2001; Grezes et al., 2001; Iacoboni et al., 1999; Johnson-Frey et al., 2003; Rizzolatti et al., 1996b). Behavioral studies have demonstrated interactions between action perception and execution (Brass et al., 2000, 2001a,b; Hamilton et al., 2004; Kilner et al., 2003) and lend additional credence to the idea of overlapping neural processes for action observation and execution. Meta-analysis of 26 functional neuroimaging studies on action representations by Grezes and Decety (2001) illustrates that extensive overlap exists between brain regions active during action observation, simulation, and execution, but also highlights the differences in active regions between these tasks. When considering differences solely between action observation and simulation, data from the studies reviewed showed that PMv is most active during action simulation and was not always reported to be active during action observation. In addition, action observation activated more temporal regions, including superior temporal gyrus (STG), that are not active during simulation, a finding the authors attribute to increased visual scene processing demands.

In the present study, we used action observation to guide action simulation. Therefore, the goal of the present study was not to dissociate action simulation from action observation, but instead to measure the effect of embodiment on action simulation constrained by simultaneous observation. Most studies of action observation and simulation have used highly familiar actions, for which there is an established motor representation that can be activated by the imagery or observation task. However, it is also possible to observe movements which are not embodied and cannot be performed. Such movements might be poorly simulated and lead to weaker activations in the simulation circuit than familiar movements. Several studies have begun to address this question and have collectively demonstrated that the action simulation circuit shows the greatest activity when an individual observes an action that he or she is able to perform, compared to observation of physically impossible movements (Costantini et al., 2005; Stevens et al., 2000), movements made by a non-conspecific (Buccino et al., 2004), or unfamiliar dance movements (Calvo-Merino et al., 2005). However, all these studies have used extreme differences in the action stimuli between conditions, comparing actions performed daily to ones which are seldom seen and never performed by the participants. For example, in the dance study, participants watched movies of performers executing a style with which the observer was expertly familiar versus a different dance style that they had never before performed. The study was therefore limited by a cross-population design and differences of physical, visual, and semantic familiarity with the movements.

In the present study, we examine the effects of embodiment on action simulation in greater detail, comparing observation of dance movements that have been recently learned and are physically familiar to observation of unlearned movements in the same style that are not physically familiar. We manipulated participants' motor experience with 2 sets of complex modern dance sequences and scanned participants once a week for 5 weeks while they learned the movements. By using a within-subject design, we avoid between-population comparisons. The test and control video stimuli were equally visually familiar. Additionally, participants in the present study were learning and observing modern dance sequences that do not have standardized verbal labels attached to the movements. Most forms of dance, including classical ballet, tap, ballroom, capoeira, square dancing, and many others, have specific words associated with individual movements that dancers combine to create sequences. However, the bulk of modern dance does not have a standard, specific, or readily identified movement lexicon. Therefore, we are able to minimize confounds of verbalization.

With these methodological gains, the present study evaluated three hypotheses concerning the modulation of cortical activity within simulation circuits. First, we hypothesized that the simulation regions, SMAr, PMv, IPL, STS, and M1, might demonstrate greater activity during observation and imagination of recently learned movement compared to visually familiar but physically unpracticed movement. Second, we hypothesized that time spent practicing movement subsequent to learning might modulate activity within brain areas involved in action resonance. Third, we predicted that simulation circuits would be modified by self-judgment of performance ability for each of the simulated movements.

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