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The handedness of imagined bodies in action and the role of perspective taking

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ABSTRACT

Past research at the nexus of motor control and perception investigated the role of perspective taking in many behavioral and neuroimaging studies. Some investigators addressed the issue of one's own vs. others' action imagination, but the possible effects of a front or a back view in imagining others' actions have so far been neglected. We report two 'single trial' experiments in which a total of 640 participants were asked to imagine a person performing a manual action – either in a front or in a back view – and then to indicate the hand used by the imagined person during movement execution. In such a task, we assume the existence of two distinct biases: a perceptual-mnemonic bias due to subjects' visual experience of others' actions, encouraging them to imagine right-handed movements, and a motor bias due to subjects' experience of self-made actions, encouraging them to imagine movements performed with the same hand as their dominant hand. We hypothesized that a greater involvement of motor representations in the back view compared to the front view could result in an increased correspondence between one's own manual preference and the hand used by the imagined agent in the former condition. The results of both experiments were consistent with this hypothesis, suggesting that while imagining others' actions we employ motor simulations in different degrees according to the perspective adopted.

1. Introduction

Many studies on the mental simulation of actions have focused mainly on the first-person perspective (Decety et al., 1994; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Leonardo et al., 1995; Lotze et al., 1999; Porro et al., 1996; Roth et al., 1996; Schubotz & von Cramon, 2004; Stephan et al., 1995) and, to a much lesser extent, on the difference between first- and third-person perspectives (Lorey et al., 2009; Ruby & Decety, 2001). Furthermore, we stress that previous research has omitted to investigate, relative to the third-person perspective, whether differences exist between imagining an agent seen frontally (front view) or an agent seen from behind (back view).

Ruby and Decety (2001) compared first-person perspective with third-person perspective simulation, requiring participants to imagine actions performed by themselves or by an agent as if seen in a three-quarter view. The activations observed during the first-person perspective condition in the left inferior parietal cortex, the left supplementary motor area, the left precentral gyrus and the right cerebellum support the idea of a functional equivalence between action execution and action imagination (Grèzes & Decety, 2001; Jeannerod, 1995). Moreover, compared to the third-person perspective, the first-person perspective showed increased activations in the left inferior parietal lobule and the left somatosensory cortex. Ruby and Decety (2001) proposed that the activation of the left inferior parietal lobule might reflect the important role of this region in programming one's own movements, as the programming can eventually be transformed in actual movements. Lorey et al. (2009) also found stronger activation in motor and motor-related areas of the left hemisphere, that is the left inferior parietal lobule, the left supplementary motor area and the left ventral premotor cortex, as well as in the right cerebellum, during first-person imagery of movements than during third-person imagery. According to Lorey et al., the left-biased activation in the first-person perspective is consistent with the left hemisphere dominance for action (see also Vogeley & Fink, 2003) and is likely to contribute to the process of differentiating between oneself and others.

In our opinion, if one assumes that the first-person (as well as egocentric) perspective and the third-person (as well as allocentric) perspective can be assimilated to respectively the front view and the back view of another person, differences relative to the degree of motor areas activation could also exist when imagining an acting person in front and back views. Some suggestions in this direction may be found in the literature. From a theoretical standpoint, Jeannerod (1994) proposed a distinction between motor and visual imagery of actions. According to Jeannerod, motor imagery refers to a first-person process involving both kinesthetic and

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visual representations, and also motor simulations of one's own body, whereas visual imagery refers to a third-person process involving mainly a visual representation of an action (see Sirigu & Duhamel, 2001; Stinear, Byblow, Steyvers, Levin, & Swinnen, 2006, for consistent empirical findings). In line with this distinction, Lorey et al. (2009) found that their participants judged imagery trials in a first-person perspective more vivid than imagery trials in a third-person perspective, a result which was accompanied by a stronger activation in motor and motor-related areas of the left hemisphere. Consistently, Jackson, Meltzoff, and Decety (2006) found that the imitation of hand and foot actions observed in a first-person perspective (with the model presented as if the camera was in the model's eyes) was initiated faster than when the actions were observed in a third-person perspective (that is, with the model facing the camera). The authors attributed their results to a greater visuospatial similarity between the imitator and the model to imitate in the first-person perspective: in this condition, in fact, the motor representation of the action should be more readily available, thus inducing a stronger pattern of activation in the motor-related structures. Jackson et al. also found that both observing and imitating actions in a first-person perspective, compared to a third-person perspective, increased activation in the sensory-motor cortex. These authors proposed that the enhanced activity in the left sensory-motor cortex could represent a consequence of the greater contribution of the motor representation in the first- than in the third-person perspective, and also suggested that the motor representation based on the former condition might involve more kinesthetic components than that based on the latter. Also, a Transcranial Magnetic Stimulation (TMS) study by Alaerts, Heremans, Swinnen, and Wenderoth (2009) showed that, in right-handed participants, observing right hand actions from an egocentric (first-person) perspective elicited higher responses in the left primary motor cortex than observing actions from an allocentric (third-person) perspective. Furthermore, although with somewhat complex patterns, effects of perspective on hand movement reaction times were found by employing hand pictures both as primes and as targets (Bruzzo, Borghi, & Ghirlanda, 2008; Vogt, Taylor, & Hopkins, 2003). In sum, these studies support the idea that the first-person perspective recruits the motor production systems more extensively than the third-person perspective, whether the actions are performed or not.

It is plausible that the stronger activation in motor and motor-related areas of the left hemisphere observed for the first- than for the third-person perspective in the previously mentioned studies could be due to the fact that they implied right limb actions or right limb action observation and imagination by right-handed participants. In fact, recent research indicates that hand action representations are differently lateralized in right- and left-handed individuals for a variety of tasks (Dassonville, Zhu, Ugurbil, Kim, & Ashe, 1997; Lewis, Phinney, Brefczynski-Lewis, & DeYoe, 2006; Solodkin, Hlustik, Noll, & Small, 2001; Willems & Hagoort, 2009; Willems, Hagoort, & Casasanto, 2010; Willems, Toni, Hagoort, & Casasanto, 2009). In particular, Willems et al. (2009) found differential and opposite lateralization of activity in the dorsal premotor cortex and the primary somatosensory cortex in right- and left-handers required to imagine performing one-handed manual actions, as compared to non-manual actions, concluding that motor imagery involves generating action plans consistent with the kinematics of actions that people would perform with their own bodies. These results suggest that motor imagery is body-specific (that is, the way a person usually performs an action is reflected in neural activation during motor imagery) rather than merely abstract. We propose that such a body-specific representation might also emerge when one imagines an action performed by somebody else, and that this representation might be modulated by the specific perspective adopted (that is, whether the imagined agent is seen from the front or from the back). In particular, we expect a greater involvement of motor circuits when imagining an agent in a back-view than in a front-view condition, in agreement with studies indicating different patterns of activation between first- vs. third-person perspective and egocentric (front-view) vs. allocentric (back-view) perspective in several tasks.

In order to test our hypothesis, we used an action-imagination task, asking participants to report the handedness of imagined agents. We employed a paradigm which imposed no constraints relative to right or left limb involvement, but rather exploited the lateralized response of participants as an index of differential involvement of distinct brain areas according to the perspective adopted. We assumed, in fact, that differential amount of matching between one's own dominant hand and the hand used by the agent in the two conditions may indicate differential activation of motor areas: specifically, a greater activity in regions involved in action planning and control in the back-view condition could result in an increased correspondence between one's own manual preference and the imagined agent's hand use, because of a more ready transfer from movement planning to – albeit simulated – movement production. Indeed, we propose that while body-specific representations are likely to affect the imagination of somebody else's actions in a back-view perspective, the effect of more abstract and/or visual representations could emerge in a front-view perspective, both left- and right-handers being exposed mostly to right-handed actions. Some evidence in this direction may be found in a recent study by Gardner and Potts (2010), who asked participants to make speeded left–right judgements about a schematic human figure. Regardless of the spatial orientation (front or back view) of the figure, consistent left-handers showed faster response times to the figure's left hemibody, while both inconsistent left-handers and right-handers showed faster response times to the figure's right hemibody. The fact that inconsistent left-handers showed facilitated performance to the figure's right hemibody may suggest a trade-off between motor and visual representations, which could result in attentional biases towards the right side of observed bodies in the absence of a strong hand preference. Interestingly, inconsistent left-handers showed a non-significant trend for faster response times to the figure's right hemibody when presented with a front-view figure, while no differences were observed when they were presented with a back-view figure, suggesting that visual representations shape others' action and body representations mainly in a front-view perspective. Gardner and Potts concluded that, even in the absence of actual or implied actions, one's own motor competency (and thus motor simulation) may contribute to others' whole body perception, consistent with previous studies indicating the role of motor simulation during the perception of body parts (for example, when deciding whether a hand is a left or right hand, observers seem to imagine their own hand moving from its actual orientation to the stimulus orientation; Ionta, Fourkas, Fiorio, & Aglioti, 2007; Parsons, 1987b, 1994).

We devised two experiments in which participants were asked to imagine another person performing a manual action in one of two conditions: in both experiments half of the participants were invited to imagine the person as seen from the front, while the other half were invited to imagine the person as seen from the back. The only difference between the two experiments is that in Experiment 1 participants had to indicate the hand used by the imagined agent by pointing at the experimenter's right or left hand in the front-view condition or by showing their own right or left hand in the back-view condition, while in Experiment 2 they had to represent the imagined action employing a manikin (provided by the experimenter) placed in the proper perspective according to the condition tested. We decided to collect a single response per participant in both experiments, assuming that the collection of more than one trial might have suffered from at least two main