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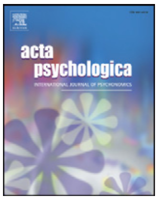

Balancing cognitive control: How observed movements influence motor performance in a task with balance constraints

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We investigated the influence of observed movements on executed movements in a task requiring lifting one foot from the floor while maintaining whole-body balance. Sixteen young participants (20–30 years) performed foot lift movements, which were either cued symbolically by a letter (L/R, indicating to lift the left/right foot) or by a short movie showing a foot lift movement. In the symbol cue condition, stimuli from the movie cue condition were used as distractors, and vice versa. Anticipatory postural adjustments (APAs) and actual foot lifts were recorded using force plates and optical motion capture. Foot lift responses were generally faster in response to the movie compared to the symbol cue condition. Moreover, incongruent movement distractors interfered with performance in the symbol cue condition, as shown by longer response times and increased number of APAs. Latencies of the first (potentially wrong) APA in a trial were shorter for movie compared to symbol cues but were not affected by cue-distractor congruency. Amplitude of the first APA was smaller when it was followed by additional APAs compared to trials with a single APA. Our results show that automatic imitation tendencies are integrated with postural control in a task with balance constraints. Analysis of the number, timing and amplitude of APAs indicates that conflicts between intended and observed movements are not resolved at a purely cognitive level but directly influence overt motor performance, emphasizing the intimate link between perception, cognition and action.

1. Introduction

Humans have a remarkable ability and tendency to imitate each other's actions, a capacity which is likely to be crucial for social interaction, skill and language acquisition and cultural evolution (Meltzoff & Moore, 1974; Miller & Dollard, 1941; Tomasello, Kruger, & Ratner, 1993). Imitation poses a complex computational problem, as it requires a transformation between two different domains, from a visual to a motor representation (Brass & Heyes, 2005). Yet, experimental evidence suggests that imitation may at least partly constitute an automatic process, as seeing another person's movement facilitates executing the same movement and interferes with performance of different movements, even if participants are instructed to ignore the other's action (Heyes, 2011). The present study extends previous research on automatic imitation tendencies, which mostly concerned relatively isolated movements of body parts (Brass, Bekkering, & Prinz, 2001; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Leighton & Heyes, 2010; Stürmer, Aschersleben, & Prinz, 2000) to movements with whole-body balance constraints. Besides addressing the general question how automatic imitation tendencies interact with postural control, anticipatory postural adjustments (APAs), required for maintaining balance, can be measured in this task and allow a more fine-grained analysis of the underlying sensorimotor–cognitive interactions.

Close links between action and perception have been postulated since the early days of psychology (James, 1890; Lotze, 1852). This proposition is supported by behavioral and neuroimaging studies on action-effect binding, showing bi-directional associations between movements and their sensory consequences (Greenwald, 1970; Hommel, Musseler, Aschersleben, & Prinz, 2001; Kühn, Keizer, Rombouts, & Hommel, 2011; Kühn, Seurinck, Fias, & Waszak, 2010). As a consequence, imitation may be subserved by general mechanisms by which observing an action automatically activates neural circuits involved in performing the action oneself. Such an automatic activation could reflect actions being encoded in terms of their perceptual consequences, as proposed by ideomotor or common coding theories (Prinz, 1990), or, more generally, the result of associative learning (Brass & Heyes, 2005; Elsner, 2007; Heyes, 2001).

Behavioral evidence for this view on imitation comes from studies assessing compatibility effects between to-be-performed movements (and their sensory consequences) on the one hand and visual stimuli on the other hand. In one such study, participants had to lift either the index or the middle finger of their dominant right hand in response to a visual cue while ignoring potential visual distractors (Brass et al.,

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2001). Movements were either cued by a short movie of one finger being lifted or by a symbol ("1" or "2"). Compatibility effects were demonstrated in two ways in this study. First, responses were faster for movie cues compared to symbol cues. Second, if participants are symbolically cued to lift one finger while observing a lifting movement of a different finger, response times are longer than when symbolic cue and the movement distractor indicate the same response. Thus, even when participants were explicitly instructed to ignore it, the movie cue influenced the symbolically cued movement. The converse did not hold, that is, movements indicated by a movie cue were immune to interference by the symbolic distractor. Similar compatibility effects have also been demonstrated for movements with other body parts, such as hands, feet, or the mouth (Gillmeister et al., 2008; Heyes, Bird, Johnson, & Haggard, 2005; Leighton & Heyes, 2010; Stürmer et al., 2000), including symbolic gestures (Belot, Crawford, & Heyes, 2013; Cook, Bird, Lünser, Huck, & Heyes, 2012). A number of studies on arm and hand movements employed continuous measures to quantify automatic imitation tendencies in more detail (Bouquet, Gaurier, Shipley, Toussaint, & Blandin, 2007; Kilner, Paulignan, & Blakemore, 2003; Saby, Marshall, Smythe, Bouquet, & Comalli, 2011), demonstrating that (in)compatibility between observed and to-be-performed movements can have subtle effects on movement trajectories.

It has been proposed that bidirectional associations between actions and perception (and hence compatibility effects as discussed above) are acquired through sensorimotor experience with self-performed movements and their sensory consequences (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Brass & Heyes, 2005; Catmur et al., 2008; Hommel et al., 2001). This hypothesis was directly addressed in training studies in which participants had to respond with the hands to observed movements of the feet, and vice versa. This training led to a significant reduction in the effector-specificity of compatibility effects (Gillmeister et al., 2008) and to a reversal in neural responses during observation of hand versus foot movements (Catmur et al., 2008). Presumably, the training induced a generalization of visual action effect binding across effectors, emphasizing the role of sensorimotor experience as proposed by associative learning accounts of imitation (Brass & Heyes, 2005; Elsner, 2007; Heyes, 2001).

Summing up, there is substantial behavioral evidence that observation of task-irrelevant movements influences motor performance, and neuroimaging studies suggest that this is related to the automatic preactivation of motor programs for the corresponding actions, which may be compatible or incompatible with the to-be performed movement. However, it is currently not known whether automatic imitation tendencies and resulting compatibility effects are confined to relatively isolated movements (e.g., moving a finger or arm, or opening/closing a hand) not requiring preparatory adjustments, or whether they also occur for more complex movements, in particular movements with whole-body balance constraints.

The goal of the present study therefore is to investigate compatibility effects between observed and to-be-performed movements in a complex whole-body task: lifting one foot from the floor while maintaining balance. In order to lift one foot from the floor, it is not sufficient to activate the muscles that induce hip and knee flexion, but the whole body needs to be adjusted, shifting the weight to the opposite (standing) leg prior to the focal movement in order to maintain balance. In fact, the APA involves a preparatory movement (pushing to-be lifted foot into to the floor) which to some extent is *opposite* to the focal movement (lifting the foot). Thus, if observed movements influence motor performance by automatically activating muscles required for the focal movement (lifting the foot) without taking into account balance constraints, observing a foot lift action might actually hamper performance of the preparatory weight shift for lifting the foot on the same side. In contrast, if automatic imitation tendencies are integrated with postural control, observing a foot lift movement should facilitate lifting the ipsilateral foot and hamper lifting the contralateral foot, similar to a previous study on finger lift movements (Brass et al., 2000).

Moreover, balance constraints do not only make the motor task (and the correspondence mapping) more complex, but measuring APAs may also allow a more fine-grained temporal analysis of motor aspects of interference effects (e.g., Cohen, Nutt, & Horak, 2011). If the conflict between to-be-performed and observed movement is resolved at a cognitive level, both foot-lift responses and APAs should be delayed in incongruent conditions compared to congruent conditions. In contrast, if movement observation directly influences the motor system, as suggested by automatic imitation accounts, incongruent movement distractors should lead to wrong initial APAs (corresponding to the observed foot lift movement), which subsequently need to be corrected to lift the correct foot.

2. Material and methods

2.1. Participants

Sixteen right-handed young adults aged between 20 and 30 years (mean age: 25.4 years, SD: 3.2 years) took part after providing written informed consent and received a compensation of 10 Euro per hour. The study was approved by the Ethics Committee of the Max Planck Institute for Human Development.

2.2. Setup and data acquisition

During the foot lift task (see below), participants stood with their feet on two force plates (Kistler 9286AA, Kistler Instruments, Wintertur, Switzerland) with horizontal dimensions of 60 cm by 40 cm, in order to measure ground reaction force (GRF) separately from the two feet. Foot positions were marked by two pieces of carpet of dimensions 30 cm by 12 cm each, placed at a lateral distance of 20 cm (centers of the back edge) and an angle of 10°. Visual stimuli were back-projected to a screen placed at a distance of 150 cm in front of the force plates (projection design, F20 SX+). The size of the visual stimuli on the screen was 72 cm by 54 cm (size of the symbol: 7 × 8 cm), presented at a height of 40 cm above the floor.

Three-dimensional kinematic data were recorded using an 8-camera optical motion capture system (Vicon Motion Systems, Oxford, UK). Reflective markers were attached to relevant landmarks on the participant's body. Only data from the markers on the toes, sacrum and seventh cervical vertebrae (C7) are used in the present analysis. Kinematic and force plate data, were recorded continuously during each block of trials (see below) at sampling rates of 100 Hz and 1000 Hz, respectively.

For a second experiment (finger lift task, see below), participants were comfortably seated at a table, with a computer screen at a distance of about 50 cm from their eyes, the dominant right hand resting on a custom-built response, which recorded finger lift movements using infra-red light sensors. Visual stimuli for this task were shown on the screen on a size of about 12 × 9 cm (symbol: 1 × 1 cm).

2.3. Task and procedure

Experimental programming was done in Matlab (Matlab R2011b, MathWorks, Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007). The foot lift experiment consisted of a *symbol cue* and a *movie cue* condition, presented in separate blocks. In both conditions, two lower legs and feet were continuously displayed on the projection screen (Fig. 1, top panel). In the *symbol cue* condition, the letter L or R was presented between the feet, the task being to lift the corresponding (left or right) foot from the force plate. The symbolic cue was either shown without concurrent foot movement (baseline; Fig. 1, bottom center), with a foot lift movement on the same side (congruent; Fig. 1, bottom left), or with a foot lift movement on the opposite side (incongruent; Fig. 1, bottom right). In the *movie cue* condition, an animated sequence showing a foot lift was presented, and the task was to