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Motor priming by movement observation with contralateral concurrent action execution

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ABSTRACT

In the present study, the influence of simultaneous action execution on motor priming was investigated during movement observation using a simple-reaction task. Although previous studies have reported various effects of priming on motor performance, it has not yet been clarified how an additional source conveying kinetic information would modulate the priming effects. In the experiment, participants were asked to respond to an auditory cue by flexing their wrist while observing a line movement, which was slowly swinging like an inverted pendulum. In addition to the observation of line movement, the participants executed wrist flexion-extension actions synchronizing with line movement. The hand involved in pre-response wrist action varied with the priming condition: no movement execution (observation only), contralateral hand, and ipsilateral hand. In the contralateral condition, the stimulus-response congruency of movement direction was conflicted depending on the frame of reference (visual vs. anatomical coordinates). We found that all three priming conditions produced the compatibility effect, and the effect size did not differ between them. Importantly, in the contralateral condition, participants responded faster when the direction of line movement was congruent with the response movement in the anatomical coordinates. That is, the reaction time was shorter when pre-response action execution was in the flexion phase, even though the direction of observed movement and the response action were incongruent from the participants' view. These results suggest that kinetic information has a great contribution to the motor priming system, which can reverse the visionbased compatibility effect.

1. Introduction

In recent years, it has been well established that movement observation significantly affects both action execution and actionrelated activation in the brain. This is referred to as motor priming or automatic imitation (Bertenthal, Longo, & Kosobud, 2006; Boyer, Longo, & Bertenthal, 2012; Brass, Bekkering, & Prinz, 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Edwards, Humphreys, & Castiello, 2003; Heyes, 2011; Liepelt & Brass, 2010). Motor priming is modulated by stimulus-response compatibility (S-R compatibility), which represents the degree of sharing movement components, including location, direction, and intention (e.g.,

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Bosbach, Prinz, & Kerzel, 2005; Brass et al., 2001; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Dolk et al., 2014; Fitts & Seeger, 1953; Hommel, 1993; Liepelt, Cramon, & Brass, 2008; Simon & Rudell, 1967). Response accuracy and latency are enhanced by stimulus-response congruency with regard to a specific dimension of the observed components. Neuroimaging and neurophysiological studies report that the observation of action activated brain regions associated with the execution of that action (e.g., Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Decety et al., 1994; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2001; Gazzola & Keysers, 2009; Iacoboni et al., 1999; Shmuelof & Zohary, 2008; Vigneswaran, Philipp, Lemon, & Kraskov, 2013). Such studies indicate that action observation and execution share common resources in the brain, providing an individual with the ability to understand, anticipate, and discriminate the actions and intentions of others (Blakemore & Frith, 2005). In the present study, to further understand the nature of motor priming, we investigated influences of simultaneous movement execution synchronized with a presented stimulus on S-R compatibility effects.

Previous studies have extensively investigated the influence of S-R compatibility on subsequent and ongoing action execution (Callan, Klisz, & Parsons, 1974; Hasbroucq & Guiard, 1991; Kornblum, 1994; Riehle, Kornblum, & Requin, 1997; Vainio & Mustonen, 2011). Simon and colleagues reported an effect on simple reaction-time performance when an imperative tone and a response hand shared the same spatial location, even if participants crossed their hands (Simon, Hinrichs, & Craft, 1970; Simon & Rudell, 1967). Hommel (1996) confirmed that this facilitative compatibility effect was not produced by interhemispheric connections, but by cognitive processing. Brass et al. (2001) used images of hands and a finger motion response in a simple reaction-time paradigm. In this study, S-R compatibility was greater when the direction of the finger response was congruent with that of finger action in the picture than when the response was congruent with a spatial location of the stimulus or symbol. This compatibility effect persisted when hand images were vertically flipped, suggesting that action observation was more closely linked to action execution than spatial location of movement or symbolic cues. Liepelt et al. (2008) demonstrated a compatibility effect induced by the perception of action intention, without completion of the movement. Furthermore, Kilner, Paulignan, and Blakemore (2003) demonstrated that repetitive straight limb movements were interfered by observing another individual performing a motion in an incongruent (orthogonal) direction. These studies have shown that various properties of stimulus modulate action execution.

The modulation of action execution based on S-R compatibility is consistent with ideas of shared representation between action observation and execution (Blakemore & Frith, 2005; Brass & Heyes, 2005; Heyes, 2011). James introduced a theory of ideomotor action, which assumed the image of action is constituted by sensory feedbacks of the action (James, 1890). Greenwald (1972) developed this theory and defined ideomotor compatibility as the extent to which a stimulus corresponds to sensory feedback from its required response. Prinz (1997) proposed a common coding theory, in which both action stimulus and response are encoded in a commensurable format. The common action concept therefore details the automatic activation of a response code following the presentation of a related stimulus. Craighero, Bello, Fadiga, and Rizzolatti (2002) transitioned the theory of ideomotor action from a psychological to neurophysiological setting. This theory of automatic imitation also provides an explanation for the close link between action observation and execution (Heyes, 2011). Such concepts and theories are still investigated with regard to their functional independency (Bertenthal et al., 2006; Boyer et al., 2012).

Such action representation might enable the induction of the priming effect without observation of actual human action. Edwards et al. (2003) indicated that visualization of the full "biological motion" is not required for priming the representation of an action. Bouquet and colleagues reported that non-biological dot movements induce sufficient motor interference while the effect size is smaller than that of biological dot movements, which represented human motion in a point-light display (Bouquet, Gaurier, Shipley, Toussaint, & Blandin, 2007; but see Jansson, Wilson, Williams, & Mon-Williams, 2007; Stanley, Gowen, & Miall, 2007). Furthermore, Kupferberg et al. (2012) reported that a robot was able to induce motor interference if it had a human-like arm configuration. These studies on the one hand emphasize the importance of biological feasibility of visual stimuli, such as bell-shaped movement velocity and joint-based configuration, for motor priming, but on the other hand, they suggest that the complete biological feasibility is not necessitated to obtain the priming effect.

Based on these studies, it would be possible that an additional source associating a visual stimulus with human action would modulate the priming effects. To test this possibility, we investigated whether concurrent movement execution modulates the compatibility effect induced by visual stimulus. Executing action may provide kinetic information that includes motor commands and proprioceptive feedbacks. If observation and execution of movements activate common representations, the two different sources can interact with each other in activation of the representation and its effects on motor performance (Chinellato, Castiello, & Sartori, 2015). In clinical practice, it is important to understand the influence of simultaneous movement observation and movement execution on the production of contralateral hand movements. Mirror therapy is one of effective treatments for phantom pain and hemiparesis, wherein patients have the impression that their affected hand is moving in a mirror by moving the contralateral non-affected hand. (Altschuler et al., 1999; Dohle et al., 2009; Invernizzi et al., 2013; Ramachandran, Rogers-Ramachandran, & Cobb, 1995). Dohle, Kleiser, Seitz, and Freund (2004) reported that the observation of mirror movements induced additional cortical activations corresponding to the observed image. Moreover, Garry, Loftus, and Summers (2005) demonstrated that the observation of mirrored hand movements, concurrent with the execution of hand movements, increased the amplitude of motor evoked potentials (MEP). These findings indicate that corticospinal system in the hemisphere ipsilateral to the movement hand could be primed by observing the mirror image of a moving hand, even when the movement image is spatially reversed to the primed movement. However, it remains unclear how motor priming brought by concurrent movement execution modifies behavioral performance.

In terms of the frame of reference, there would be a conflict between observed and executing movements in a particular situation, and we may have to settle it. To interpret presented visual stimuli, we can use several frames of reference (coordinate systems), including the reference frames of the external space (visual coordinates) and the body (anatomical coordinates). These two types of frame of reference encounter conflict, for example, when the observed movement is performed by an agent facing the observer, when

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