



Observation of interactive behavior increases corticospinal excitability in humans: A transcranial magnetic stimulation study



Tsuyoshi Aihara^{a,b}, Shinji Yamamoto^c, Hiroataka Mori^a, Keisuke Kushiro^a, Shintaro Uehara^{d,e,*}

^a Graduate School of Human and Environmental Studies, Kyoto University, Yoshida-Nihonmatsu-cho, Sakyo-ku, Kyoto 606-8501, Japan

^b Faculty of Medicine, Yamaguchi University, 1-1-1 Minamikogushi, Ube, Yamaguchi 755-8505, Japan

^c School of Health and Sport Sciences, Osaka University of Health and Sport Sciences, 1-1 Asashirodai, Kumatori-cho, Sennan-gun, Osaka 590-0496, Japan

^d Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology, 1-4 Yamadaoka, Suita, Osaka 565-0871, Japan

^e The Japan Society for the Promotion of Science, 5-3-1 Kojimachi, Chiyoda-ku, Tokyo 102-0083, Japan

ARTICLE INFO

Article history:

Received 4 February 2015

Revised 3 August 2015

Accepted 14 September 2015

Available online 29 September 2015

Keywords:

Action observation

Mirror neuron system

Social cognition

Human-interactive behavior

Transcranial magnetic stimulation

Corticospinal excitability

ABSTRACT

In humans, observation of others' behaviors increases corticospinal excitability (CSE), which is interpreted in the contexts of motor resonance and the "mirror neuron system" (MNS). It has been suggested that observation of another individual's behavior manifests an embodied simulation of his/her mental state through the MNS. Thus, the MNS may involve understanding others' intentions of behaviors, thoughts, and emotions (i.e., social cognition), and may therefore exhibit a greater response when observing human-interactive behaviors that require a more varied and complex understanding of others. In the present study, transcranial magnetic stimulation was applied to the primary motor cortex of participants observing human-interactive behaviors between two individuals (c.f. one person reaching toward an object in another person's hand) and non-interactive individual behavior (c.f. one person reaching toward an object on a dish). We carefully controlled the kinematics of behaviors in these two conditions to exclude potential effects of MNS activity changes associated with kinematic differences between visual stimuli. Notably, motor evoked potentials, that reflect CSE, from the first dorsal interosseous muscle exhibited greater amplitude when the participants observed interactive behaviors than when they observed non-interactive behavior. These results provide neurophysiological evidence that the MNS is activated to a greater degree during observation of human-interactive behaviors that contain additional information about the individuals' mental states, supporting the view that the MNS plays a critical role in social cognition in humans.

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1. Introduction

The ability of understanding the intentions underlying others' behaviors, thoughts, beliefs, and emotions (i.e., social cognition) is essential for proper human interactions in society. The "mirror neuron system" (MNS) has been suggested to play a critical role in social cognitive processes. The MNS, a neural network in the

brain, is activated both when a person performs an action and when the person observes another individual performing the same action. Previous human brain imaging studies demonstrated that observing another's behavior activated the inferior parietal lobule, the inferior frontal gyrus and the adjacent ventral premotor cortex (BA6) (c.f. Buccino et al., 2004). Thus, these regions have been suggested to be key nodes of the MNS (Buccino et al., 2004; Caspers, Zilles, Laird, & Eickhoff, 2010; Gazzola & Keysers, 2009; Grèzes & Decety, 2001; Iacoboni & Dapretto, 2006; Iacoboni et al., 1999), and are theoretically suggested to function as if mirroring the mental state of another person, which supports human understanding of other people (Gallese, Keysers, & Rizzolatti, 2004; Gallese & Sinigaglia, 2011; Iacoboni & Dapretto, 2006; Iacoboni et al., 2005; Oberman, Pineda, & Ramachandran, 2007; Rizzolatti & Craighero, 2004; Rizzolatti & Fabbri-Destro, 2008).

A human often observes interactive behaviors between other individuals. In this situation, one needs to comprehend the mental

Abbreviations: ADM, abductor digiti minimi muscle; CSE, corticospinal excitability; EHI, Edinburgh Handedness Inventory; EMG, electromyogram; FDI, first dorsal interosseous muscle; IND-D, individual-dynamic; IND-S, individual-static; INT-D, human interactive-dynamic; INT-S, human interactive-static; MNS, mirror neuron system; MEP, motor evoked potential; M1, primary motor cortex; rMT, resting motor threshold; TMS, transcranial magnetic stimulation.

* Corresponding author at: Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology, 1-4 Yamadaoka, Suita, Osaka 565-0871, Japan.

E-mail address: s.uehara@nict.go.jp (S. Uehara).

state of more than one person, which requires multiple and complex processes for social cognition. Considering the abovementioned properties of the MNS, we hypothesized that MNS activity increases while a person is observing behavior by another person interacting with others, compared to that while observing non-interactive individual behavior.

Although several previous studies have investigated changes in MNS activity by observing human-interactive behaviors with neurophysiological experiments, a clear conclusion has not yet been obtained. In an electroencephalography study, [Oberman et al. \(2007\)](#) showed that mu suppression, putatively reflecting activity in the MNS, was greater when participants observed human-interactive behaviors (i.e., three people tossing a ball to one another) than when they observed non-interactive behavior (i.e., each individual tossing a ball up in the air). [Bucchioni, Cavallo, Ippolito, Marton, and Castiello \(2013\)](#) also indicated, by using transcranial magnetic stimulation (TMS), that activity in the MNS was enhanced during the observation of human-interactive behaviors (i.e. an actor passing a ball to a partner) rather than individual behavior (i.e. an actor throwing a ball against a wall). However, other previous studies using TMS could not find clear evidence of changes in MNS activity according to the type of interactive behaviors ([Donne, Enticott, Rinehart, & Fitzgerald, 2011](#); [Enticott, Kennedy, Bradshaw, Rinehart, & Fitzgerald, 2011](#)). The difference in these findings may have originated from uncontrolled movement kinematics in presented visual stimuli. Indeed, each study used kinematically different movements for visual stimuli of interactive and non-interactive behaviors. Notably, MNS activity changes according to kinematic differences in the movement of presented visual stimuli ([Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995](#)). Thus, complex processes involved in social cognition and differences in the kinematics of presented images can affect MNS activity, which might lead to the incongruity observed in the above findings.

In the present study, we used TMS to investigate whether MNS activity changed while the participants were observing human-interactive behaviors or non-interactive behavior. We carefully controlled the kinematics of the visual stimuli, and excluded the effect of kinematic differences on MNS activity. TMS of the primary motor cortex (M1) produces a muscle response (motor evoked potential; MEP) corresponding to a stimulus site in the M1 that can be recorded via an electromyogram (EMG). Changes in MEP amplitude during observing others' behavior indicate increased corticospinal excitability (CSE) and can be used as a putative measure of changes in the MNS (the premotor cortex and the adjacent inferior frontal gyrus) activity in humans ([Enticott et al., 2012](#); [Fadiga et al., 1995](#); [Gangitano, Mottaghy, & Pascual-Leone, 2001](#); [Maeda, Kleiner-Fisman, & Pascual-Leone, 2002](#)). Here, we hypothesized that MEPs in specific hand muscles (first dorsal interosseous; FDI, abductor digiti minimi; ADM) would be greater when observing interactive behaviors under conditions where the kinematic information of visual stimuli was carefully controlled. Through our experiments, we aimed to determine whether changes in MNS activity depend on whether the participants observed human-interactive or non-interactive behaviors.

2. Experimental procedures

2.1. Participants

Thirteen right-handed healthy men (mean age \pm standard error; S.E. = 24.2 ± 0.9 years) participated in this study. Handedness was assessed using the Edinburgh Handedness Inventory (EHI) ([Oldfield, 1971](#)). All the participants reported normal or corrected to normal visual acuity and had no history of medical or neurological

disorders. Written informed consent was obtained from each participant prior to the experiment. This study was approved by the Ethical Committee of the Graduate School of Human and Environmental Studies, Kyoto University, and was performed following the principles and guidelines of the Declaration of Helsinki (1975).

2.2. Experimental settings and visual stimuli

The participants were instructed to observe 9-s video clips (30 frames per second) of hand movements while seated in a comfortable recliner chair with their right hand resting on the armrest. Video clips were presented on a computer screen (26 cm in height and 32 cm in width) 100 cm away from the participants. Each video clip consisted of three phases including fixation, action observation, and catch phases (comprising one experimental trial, [Fig. 1A](#)). During the fixation phase, a white fixation cross was presented on a black screen for 3 s, followed by the action observation phase when one of several kinds of images (see below) were presented for 5 s. Finally, during the catch phase, two words related to a prior image in the action observation phase were presented for 1 s. Video clips were edited with Corel VideoStudio Pro X4 software (Corel Japan Ltd., Tokyo, Japan).

Images presented in the action observation phase were composed of a picture and a movie covering the left side (one-third of the image) and right side (two-thirds of the image), respectively ([Fig. 1B](#)). We prepared two experimental factors, human interaction (human interactive [INT]/individual [IND] behavior) and image type (dynamic [D]/static [S] image). Then, we created images suitable for the four different conditions by combining these two factors (human interactive-dynamic [INT-D], individual-dynamic [IND-D], human interactive-static [INT-S], and individual-static [IND-S]; [Fig. 1C](#)).

For images of each condition, we prepared images of four different types of behavior by compounding a picture and a movie (i.e., we created 16 types of images in total) to eliminate the possible effect of a specific behavioral type on MNS activity. The four images of the human interactive-dynamic (INT-D) condition included a hand reaching toward an apple or a cup in another's hand, and passing an apple or a cup to another's hand. The images of another hand provided information that two people were going to interact with each other through dynamic actions. Similarly, another four images of the individual-dynamic (IND-D) condition included a hand reaching toward an apple or a cup on a dish, and passing an apple or a cup to a dish. By replacing the other and in the left side of the images with a dish, we created the situation where one person was going to perform an individual behavior. Importantly, we used the same movies of hand actions between the INT-D and IND-D conditions for each behavioral type (e.g., the movie of a hand reaching toward an apple in another hand or a hand reaching toward an apple on a dish was the same). This excluded the effect of kinematic differences between the INT-D and IND-D conditions on MNS activity. Furthermore, the picture on the left one-third of the image was gradually covered with a gray mask during the action observation phase ([Fig. 1A](#)) ([Turella, Tubaldi, Erb, Grodd, & Castiello, 2012](#)). The pictures were then completely covered by the mask upon TMS application (see below). By concealing the pictures on the left side and the border between pictures and movies, we hid the inconsistency of the pictures and movies in the images. A previous animal study demonstrated that a subset of mirror neurons is activated during the observation of another's actions, even when the final part of the action is hidden and can therefore only be inferred ([Umiltà et al., 2001](#)). Therefore, in our experiment, we assumed that the human MNS would also exhibit changes in activity when observing another's behavior even if the final part of the behavior was hidden.

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