



The role of handedness-dependent sensorimotor experience in the development of mirroring



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

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

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

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

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

HIGHLIGHTS

- Mirror properties can be modified through sensorimotor experience.
- We studied the effect of handedness on this property by using imitative response.
- Left-handers could imitate right-handed actions faster than left-handed actions.
- Right-handers showed no difference in responses to left- and right-handed actions.
- The handedness of the observer likely affects the development of the mirroring.

ARTICLE INFO

Article history:

Received 24 June 2014

Received in revised form

11 September 2014

Accepted 9 October 2014

Available online 23 October 2014

Keywords:

Handedness

Motor imitation

Mirror system

Mirror property

Sensorimotor associative experience

ABSTRACT

In daily life, we often try to learn motor actions by imitating others' actions. Motor imitation requires us to simultaneously map an observed action onto a motor program used to perform that action. This sensorimotor associative experience can plastically modulate the mirror property of the human mirror system, which has a role in matching observed actions directly with the observer's motor programs, to enhance the association between observed and performed actions. In the present study, we investigated the effects of handedness on the mirror property. Healthy left- and right-handed individuals performed a motor imitation task. They were required to imitate hand actions with their dominant hand as quickly and accurately as possible in response to pictures of a left and right hand. Reaction times (RTs) for imitating the hand actions were evaluated. Under the condition where the hand pictures were presented as if facing the participant, we found that, in left-handed participants, RTs for imitating right-handed actions were significantly shorter than those for imitating left-handed actions. Under the same conditions in right-handers, similar differences in RTs when presented left- and right-handed actions were not observed. These findings demonstrate that the imitative responses for left- and right-handed actions are differently facilitated depending on the handedness of the observer, indicating an effect of handedness on the development of mirror systems. The mirror property in left- and right-handers is likely modulated in a different manner by different sensorimotor associative experiences throughout their daily lives.

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1. Introduction

In daily life, we often observe and imitate others' actions to effectively learn those motor actions. The process for imitating

actions requires us to map an observed action onto a motor program used to perform that action. This mapping process could be mediated by the human mirror system, a neural network of brain regions that directly matches observed actions onto the observer's motor programs [1–4]. The mirror system is considered to match observed-effector actions onto the identical and similar motor programs to be performed [5–7]. Therefore, the sight of an action primes motor representation for an imitative action [8], which enables us to imitate actions more quickly when observed and intended actions are identical compared to non-identical [9].

* 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. Tel.: +81 80 9045 9528.

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

Recently, it is argued that the mirror system is forged by domain-general processes of associative learning in the course of individual development, and not an innate endowment [10,11]. Supporting this view, a number of studies suggested that the property of matching observed actions with motor programs (mirror property) is not fixed, but is rather flexibly modified through sensorimotor associative experience [3,4,12–15]. For example, after the training of performing one action while observing another action, the mirror system begins to match this observed action onto the motor program of the simultaneously performed action [13]. Another study showed that a brief period of incompatible sensorimotor associative experience, where participants responded to observing hand opening by closing their hands and to hand closing by opening their hands, abolished the previous property of motor imitation. Therefore, imitative responses in incompatible trials can be performed as fast as those in compatible trials [14]. These lines of evidence indicate that the mirror property can be modified when visual input of actions and motor output are experienced simultaneously [4], and suggest that daily experience in imitating others' actions would be a powerful driver of modifying the mirror property of the human mirror system.

In the present study, we investigated the effect of handedness on the mirror property by evaluating response times for the imitation of several hand actions. It is well known that the population of left-handers in humans is fewer than that of right-handers [16,17]. Therefore, left-handers have a greater opportunity to imitate actions of larger population of right-handers throughout their daily lives. Based on this view, we hypothesized that the mirror system in left-handers possessed the mirror property of matching actions performed by right-handers, rather than those by left-handers, onto their own-handed motor programs. In this case, left-handers should show faster response times for imitating actions of right-handers than those of left-handers. With applying the above viewpoint to right-handers, we can expect that all actors (both left- and right-handers) should show a stronger tendency to imitate right-handed actions more quickly. To verify this hypothesis, we measured reaction times (RTs) of left-handers and right-handers cross-sectionally, in a motor imitation task.

2. Materials and methods

2.1. Participants

Eight left-handed (all male; mean age $\pm$ S.D. = 22.1 ± 2.0 years) and eight right-handed (one female; 23.1 ± 3.4 years) healthy volunteers participated in this study. Their handedness was assessed using the Edinburgh Handedness Inventory (EHI) [18]. The mean EHI score was -58.5 ± 22.5 and 93.6 ± 5.3 (mean $\pm$ S.D.) for the left- and right-handers, respectively. All participants provided written informed consent. The Ethical Committee of the Graduate School of Human and Environmental Studies, Kyoto University, approved the study. The experiment was carried out following the principle and guidelines of the Declaration of Helsinki (1975).

2.2. Motor imitation task

We prepared a choice motor imitation task requiring the participants to imitate simple hand-finger actions as quickly and accurately as possible with their dominant hand. A computer screen (26 cm in height and 32 cm in width) was set in front of the participants. The participants performed the task while seated with their dominant hand pronated and resting on the armrest of the chair. Four different pictures of simple finger actions, abduction of index or little finger in the left or right hand (action stimuli in Fig. 1A), were presented on the screen during experimental trials

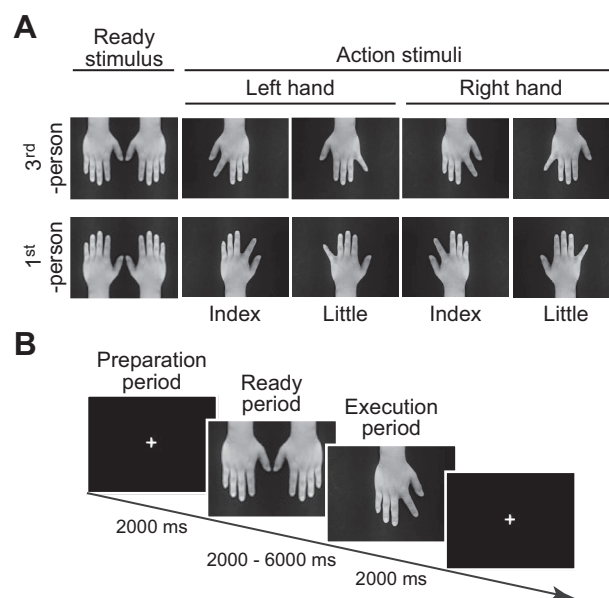


Fig. 1. Visual stimuli (A) and a trial sequence (B) for the motor imitation task. Each trial consisted of a 2000-ms presentation of a preparation stimulus, followed by the presentation of a ready stimulus for a random duration of 2000–6000 ms, and a further 2000-ms presentation of one of four kinds of pictures of finger abductions (action stimuli; left-index, left-little, right-index or right-little). The perspective (3rd or 1st person perspectives) of pictures in the ready stimulus and action stimuli was kept identical through trials in a block.

in both 3rd (as if facing the other person) and 1st (the viewpoint of oneself) person perspective conditions. Each trial consisted of a 2000-ms presentation of a white fixation cross on the black screen (a preparation stimulus), followed by the presentation of a static two-handed picture for a random duration of 2000–6000 ms (a ready stimulus), and finally the presentation of one of the four action stimuli for 2000 ms (Fig. 1B). The participants were required to perform the same finger action as shown in the presented picture (abduction of the index or little finger) with their dominant hand immediately after the action stimulus was presented. After each trial was completed, the participants quickly set their hand back to the starting posture to prepare for the next trial.

The experiment for each participant consisted of 6 blocks, and each block was composed of 32 trials (8 trials for each of four action stimuli). The participants conducted 3 blocks in one perspective condition, and the remaining 3 blocks in the other perspective condition. The order of conditions was counter-balanced among the participants. An inter-block interval of about 1 min was set as a break time. The presentation order of action stimuli in each block was randomized. The experimental task was controlled by custom-made program build by LabVIEW 8.5 (National Instruments, Japan).

2.3. Electromyography

During the experiment, we recorded surface electromyograms (EMGs) from the first dorsal interosseous (FDI) and abductor digiti minimi (ADM) of the participants' dominant hand with surface electrodes (GA-U410, TEAC, Japan). The disposable self-adhesive electrodes (Vitrode M, NIHON KOHDEN, Japan) were placed on the epicondylus lateralis humeri of the dominant hand. EMG signals were amplified 1000 times with an amplifier (BA1104, TEAC, Japan), and stored on a personal computer for later offline analysis via an A/D converter (Powerlab, ADInstruments Japan, Japan).

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