広島大学学術情報リポジトリ Hiroshima University Institutional Repository

Title	Effect of observation combined with motor imagery of a skilled hand-motor task on motor cortical excitability: Difference between novice and expert
Auther(s)	Tsukazaki, Izumi; Uehara, Kazumasa; Morishita, Takuya; Ninomiya, Masato; Funase, Kozo
Citation	Neuroscience Letters , 518 (2) : 96 - 100
Issue Date	2012
DOI	10.1016/j.neulet.2012.04.061
Self DOI	
URL	http://ir.lib.hiroshima-u.ac.jp/00034816
Right	(c) 2012 Elsevier Ireland Ltd. All rights reserved.
Relation	



Effect of observation combined with motor imagery of a skilled hand-motor task on motor cortical excitability: difference between novice and expert

Izumi Tsukazaki^a, Kazumasa Uehara^{a,†}, Takuya Morishita^{a,†}, Masato Ninomiya^a, Kozo Funase^{a,*}

^aHuman Motor Control Laboratory, Graduate School of Integrated Arts and Sciences, Hiroshima University, 1-7-1 Kagamiyama, Higashi-Hiroshima, 739-8521, Japan
[†]Research Fellow of Japan Society for the Promotion of Science

Running head: Action observation and motor imagery

Keywords: Action observation, Motor imagery, Skilled hand-motor task, Motor cortex excitability, Novice and expert, TMS

Abstract: 151 words, Main text, references, and figure legends: 4025 words, 3 figures (250 words for each figure): 750 words, Total number of words: 4926 words

*Corresponding author:

K. Funase, Ph.D. Phone and Fax: +81 82 424 6590 E-mail: funase@hiroshima-u.ac.jp

Abstract

We examined the effects of observation combined with motor imagery (MI) of a skilled hand-motor task on motor cortex excitability, which was assessed by transcranial magnetic stimulation (TMS). Novices and experts at 3-ball cascade juggling (3BCJ) participated in this study. In one trial, the subjects observed a video clip of 3BCJ while imagining performing it. In addition, the subjects also imagined performing 3BCJ without video clip observation. Motor evoked potentials (MEPs) were recorded from the hand muscles that were activated by the task during each trial. In the novices, the MEP amplitude was significantly increased by video clip observation combined with MI. In contrast, MI without video clip observation significantly increased the MEP amplitude of the experts. These results suggest that action observation of 3BCJ increases the ability of novices to make their MI performing the task. Meanwhile, experts use their own motor program to recall their MI of the task. Action observation and motor imagery (MI) might play important roles during the early stages of motor learning of a new skilled motor task, such as playing an instrument or engaging in sporting activity, especially in novices [3,18,28,32]. In fact, it has been reported that action observation increases the excitability of the motor cortex innervating the muscles that are activated during the performance of the action being observed [10,22,33], as does during motor imagery of the action [11,16,31]. However, in the above-mentioned reports, the motor tasks were relatively simple hand-motor tasks, even for novices, such as hand grasping or wrist flexion. Moreover, efficient motor learning of a skilled hand-motor task is crucial for novices who have not been trained to perform the task in question. Experience teaches us that when we try to learn a skilled hand-motor task, we observe, imagine, and imitate the motor task being performed well by another person. MI is a covert cognitive process that involves imagining the motor task according to a forward internal model without performing any actual movements [19,23,40,41]. Therefore, it might be difficult for novices to imagine a skilled hand-motor task because they have no forward internal model of it. These facts led us to the following question: Would presenting a video depicting a skilled hand-motor task being performed well by another person to a novice enhance their MI of that action?

To explore this issue, we examined the effect of observing a video clip showing

3-ball cascade juggling (3BCJ), a skilled hand-motor task, on the subject's MI of that task. The 3BCJ is a bimanual, skillful, and cyclic hand-motor task involving the handling of 3 balls. In a previous study [17], the characteristics of 3BCJ were described as follows: "Jugglers move their hands along two more or less elliptical trajectories, one a clockwise direction and the other in an anticlockwise direction, at an average phase difference of 180°. Each ball is released at the point in the ellipse closest to the mid-sagittal line of the performer's body and caught at the point in the ellipse furthest from the mid-sagittal line. The ball is thrown toward the contralateral hand along a parabolic path. As a result, it travels along a figure-of-eight pattern (rotated by 90°)". It is therefore thought that the sensorimotor systems in both brain hemispheres including the cortical and subcortical substrates must be activated to perform 3BCJ, making it much more difficult than the simple hand-motor tasks mentioned above. Experts in 3BCJ also participated in this study so that we could compare their brain activity with that of the novices. It has been demonstrated that MI of muscle contraction enhanced the motor cortical excitability [1,11,12,20,31,42]. Thus, the effects of action observation and MI on motor cortical excitability were assessed by measuring the amplitude of the motor evoked potential (MEP) evoked by transcranial magnetic stimulation (TMS). The MEPs were recorded from the first dorsal interosseous (FDI), the abductor pollicis brevis (APB), and the abductor digiti minimi (ADM) of right hand because these muscles are activated during the ball handling process, i.e., catching, holding, and releasing a ball, involved in the 3BCJ.

Ten novices (mean age \pm SD: 21.8 \pm 3.8) and 10 experts (20.4 \pm 2.5) at performing 3BCJ, participated in the present study after giving their written informed consent. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory [26]. All experimental procedures were carried out in accordance with the Declaration of Helsinki and approved by the local ethics committee at the Graduate School of Integrated Arts and Sciences, Hiroshima University.

A magnetic stimulator (Model 200, Magstim, Whitland, UK) and a figure-of-eight coil were used to deliver the electromagnetic stimuli. Care was taken to maintain the same coil position relative to the scalp throughout the experiment. The coil was placed tangential to the scalp with its handle pointing backward and rotated approximately 45° away from the mid-sagittal line. At the beginning of the experiment, the optimal position of the coil to evoke the MEPs in FDI, APB, and ADM of right hand was found on the left side of the scalp above the motor cortex and marked on a swimming cap worn by the subjects with a soft-tip pen to ensure reliable coil placement between trials. During the trials, the area of the motor cortex corresponding to the target muscles was stimulated while the subjects were seated. The resting motor threshold of the FDI was determined and defined as the minimum TMS intensity required to produce an MEP of at least 50µV in the resting FDI muscle in five of ten trials. The TMS intensity was set to 120% of the resting motor threshold. The mean size of the control MEP for the FDI was approximately 1mV. MEPs evoked in the right APB and ADM were simultaneously recorded. All EMG signals were recorded using paired Ag/AgCl surface electrodes and amplified and filtered at bandwidths of 5Hz to 3kHz (7S12, NEC San-ei Co. Ltd., Japan). Analog EMG signals were digitized at a sampling rate of 10kHz and saved onto a computer for off-line analysis of the MEP amplitude (PowerLab system, AD Instruments Pty. Ltd., Australia). Throughout the experiments, the subjects were instructed to avoid involuntary background EMG. MEPs associated with background EMG were excluded from the data analysis.

Subjects sat on a reclining chair and were instructed to put both hands in a supinated position; i.e., the same arm position as the demonstrator in the video clip performing the tasks mentioned below, on a horizontal plate attached to the chair's armrests. A white board (120×90 cm) was placed approximately 3m in front of the subject, and a video clip was projected onto it. The video clip showed the demonstrator performing the 3BCJ or pseudo-3BCJ (p3BCJ). In the 3BCJ, the balls were in contact

with one of the subject's hands for approximately 0.3s intervals. In the p3BCJ, the demonstrator alternately and repeatedly flexed and extended the elbow joints of both arms in motions that were similar to those performed in the 3BCJ but without balls. Thus, compared to 3BCJ, the p3BCJ is a bimanual but easy hand-motor task without ball handling process. Figure 1 shows one frame each from the video clips of the 3BCJ and p3BCJ. The following five experimental conditions were investigated: 1) The subjects gazed at a small black round mark (diameter: approximately 2 cm) on the white board (control); 2) they observed a video clip of 3BCJ without MI (3BCJ obs); 3) they imagined 3BCJ while watching the video clip (3BCJ obs+MI); and 4) they imagined p3BCJ while watching the video clip (p3BCJ obs+MI); 5) they imagined their own motor performance during 3BCJ without watching the video clip (3BCJ self-MI; they wore an eye-mask during this task). These experiments were performed twice each in a random order. The subjects were instructed to imagine that they were performing the 3BCJ and p3BCJ by mirroring what they saw in the video clips and to concentrate as hard as possible during each experimental condition. To ensure that the subjects maintained their concentration, the duration of the MI was limited to approximately 60s. Before the MEP recording, MI practice sessions were carried out under all MI conditions. Approximately 10s after the MI beginning, five TMS stimuli were manually triggered at intervals of at least 5s during the MI, with careful attention paid to ensure that the TMS stimuli were not delivered during a specific movement phase of the video clip; i.e., the TMS triggers were randomly dispersed regardless of the movement phase during the MI trial. A total of 10 MEPs were recorded in each condition.

Figure 1 here

In the MI conditions, the subjects were asked to evaluate the quality of their MI using a 100mm visual-analogue scale (VAS) sheet just after each MI trial, i.e., 3BCJ obs+MI, p3BCJ obs+MI, and 3BCJ self-MI. The subjects marked a short line on a VAS sheet labeled from 0 (no imaging) to 100mm (vivid image) corresponding to the vividness of their MI.

Two-way repeated measures ANOVA was carried out for analyses of VAS scores (group × condition). As a first step for analyses of MEP amplitude, repeated measures MANOVA (group × condition × muscle) was carried out. If the interactions among these conditions were found, two-way repeated measures ANOVA was subsequently carried out for analyses of MEP amplitude. And Bonferroni's post-hoc test was used for multiple comparisons. The criterion for statistical significance was p<0.05. All data are

expressed as the mean±SD.

Figure 2 shows the mean VAS scores (mm) for the novices and experts during the "3BCJ obs+MI", "p3BCJ obs+MI", and "3BCJ self-MI". Although there was no significant difference among the conditions ($F_{2,36}=0.45$, p=0.64), a significant difference was detected between the subject groups ($F_{1,18}=21.50$, p<0.01). The interaction between group and condition was significant ($F_{2,36}=4.71$, p<0.05). Among the experts, the post-hoc test detected significant differences between the "3BCJ obs+MI" and "3BCJ self-MI" (p<0.01), and the "p3BCJ obs+MI" and "3BCJ self-MI" (p<0.01).

Figure 2 here

Figure 3 shows the mean MEP amplitude (% of control) recorded in the FDI, APB, and ADM in all experimental conditions in the novices (A) and experts (B). The mean MEP amplitude was separately analyzed in each subject group, because the interaction between group and condition was revealed by MANOVA ($F_{3.54}$ =8.405, p<0.01). Although, there were no significant differences among the muscles (novice: $F_{2,27}$ =0.117, p=0.89; expert: $F_{2,27}$ =1.19, p=0.32), significant differences among the conditions (novice: $F_{3,81}$ =11.29, p<0.01; expert: $F_{3,81}$ =24.70, p<0.01) were detected in both subject groups. No interactions between muscle and condition were found in both subject groups (novice: $F_{6,81}$ =0.21, p=0.97; expert: $F_{6,81}$ =1.08, p=0.38). Among the novices, the post-hoc test detected significant differences between the "3BCJ obs" and "3BCJ obs+MI" (p<0.01), the "3BCJ obs+MI" and "p3BCJ obs+MI" (p<0.01), and the "3BCJ obs+MI" and "p3BCJ obs+MI" (p<0.01), and the "3BCJ obs+MI" and "3BCJ self-MI" (p<0.01). Meanwhile, among the experts, the post-hoc test detected significant differences between the "3BCJ obs" and "3BCJ self-MI" (p<0.01), the "3BCJ obs+MI" and "3BCJ self-MI" (p<0.01), and the "p3BCJ obs+MI" (p<0.01), the "3BCJ obs+MI" (p<0.01).

Figure 3 here

The main findings of the present study were as follows; 1) the VAS scores of the experts were higher than those of the novices, and in the experts, that of "3BCJ self-MI" was higher than other conditions, 2) Among the novices, the highest mean MEP amplitude was observed in the "3BCJ obs+MI", 3) among the experts, the highest mean MEP amplitude was detected in the "3BCJ self-MI", and 4) changes in MEP amplitude of the 3 muscles showed the similar pattern in each condition. These results suggest that the observation combined with MI of the 3BCJ effectively enhances motor cortical

excitability in novices. In contrast, in the experts who already had an internal model of 3BCJ, their motor cortical excitability was effectively enhanced according to their own MI without the observation.

In previous TMS studies of action observation, cortical excitability was increased during particular movement phases of simple motor tasks due to muscle activation [16,33]. In contrast, 3BCJ is a bimanual skillful motor task involving the simultaneous handling of 3 balls. Thus, it might require broad activation of the sensorimotor system by several sources of afferent information; i.e., vision, muscle afferent information, kinematic sensation, tactile sensation, etc. In fact, recent brain imaging studies have reported that the performance of a sensorimotor task, such as manipulating objects with one hand, activated numerous areas in the frontal (primary motor, dorsal and ventral premotor, supplementary motor, and cingulate motor), parietal (primary and secondary sensory, superior parietal lobule, and inferior parietal lobule), and occipital (primary and secondary visual) cortical areas, as well as the subcortical substrates (basal ganglia, thalamus, and cerebellum) [6,8,9,13,14,21,29,37]. Due to the complexity of 3BCJ as a bimanual sensorimotor task, it must require the activation of sensorimotor systems in both brain hemispheres including the cortical and subcortical substrates. Based on the broad brain activity produced by the complexity of 3BCJ and MI of the task, it could be thought that the MEP amplitude was constantly changing during MI of the task. Therefore, we presume that the discrepancies regarding movement phase dependence between previous studies [16,33] and the present study can be attributed to the characteristics of the motor task; i.e., whether it is simple or difficult for novices. In the present study, furthermore, the TMS triggers were randomly dispersed regardless of the movement phase during the MI trials. This means that MEPs were not evoked during a specific movement phase. If the changes in MEP amplitude were related to a particular movement phase, this phase-dependent effect would be attenuated by the random trigger method employed in the present study. Consequently, it would have been difficult to produce significant changes in MEP amplitude among the experimental conditions. However, during the MI trials we detected significant changes in MEP amplitude among the experimental conditions in both the novices and experts. Therefore, it is considered that the enhancement of cortical excitability was not dependent on the specific movement phase of 3BCJ during MI.

Brain imaging studies have provided evidence for a human mirror neuron system (MNS) in the inferior frontal and inferior parietal cortices that is activated during the grasping observation and execution paradigms [13,29]. Furthermore, magnetoencephalography studies have also reported that the motor cortex is

subsequently activated after the activation of the inferior frontal cortex during both movement observation and imitation [24,25], indicating that the motor cortex is involved in the human MNS. Several TMS studies have shown that the motor cortex is activated as part of the human MNS [10,11,22,36]. However, in TMS studies demonstrating activation of the MNS during action observation, the instructions given to the subjects regarding the action observation with or without MI were vague in most cases. There is a possibility that subjects unconsciously generate MI during action observation. Thus, providing clear instructions to subjects; i.e., explaining whether they should perform the action observation with or without MI, is quite important for TMS studies that aim to demonstrate the effect of the human MNS on motor cortical excitability. Actually, active observation (learning a motor task through observation) effectively increased the motor cortical excitability than passive observation (merely observing a motor task) [30]. In the present study, although observation of the 3BCJ without MI hardly affected the MEP amplitude, a combination of observation and MI of the 3BCJ significantly augmented the MEP amplitude of the novices. Recently, it was reported that cortical excitability as assessed by MEP was significantly enhanced by action observation combined with MI during elbow movement [33]. In addition, brain imaging studies have shown that the brain regions activated by observation, MI, and

movement overlap in the supplementary motor area, premotor cortex, superior parietal lobe, cingulate gyrus, and cerebellum [7,15], which are involved in the human MNS. Therefore, action observation combined with MI could efficiently activate the MNS and increase motor cortical excitability in the novices. We suppose that the discrepancy concerning to the effect of action observation on MEP amplitude between the previous studies and the present study is attributed to the difference of instruction to the subjects, i.e., action observation with or without MI. Interestingly, the "p3BCJ obs+MI" did not enhance motor cortex excitability in either subject group. The p3BCJ is a bimanual easy hand-motor task, in which the actions involved in 3BCJ are performed without balls. It is reasonably thought that lack of the ball handling process in the p3BCJ did not affect the MI for catching and releasing a ball. In addition, we suppose that the p3BCJ did not strongly activate the MNS because of its meaningless nature, because the MNS is involved in the recognition and understanding of observed tasks [2,38].

It has been reported that the cortical output maps of the hand muscles during a serial reaction time test became progressively larger until explicit knowledge of reaction cue order, i.e., motor memory of finger movement sequence, was achieved, and then, they returned to their baseline topography [27]. In the present study, the experts were almost able to perform 3BCJ unconsciously and automatically, indicating that they have

acquired the explicit motor memory of 3BCJ. It is thought that the experts recalled their MI of 3BCJ, i.e., "3BCJ self-MI", which would have been stored as a motor memory, and that this motor memory activated the MNS [34,35]. And also, their high VAS scores in the "3BCJ self-MI" indicate their explicit motor memory of 3BCJ. Actually, the MNS is activated during the observation of a trained task compared with its activation during the observation of an untrained task in experts [4,5]. In contrast, the MNS was activated more during the observation of non-practiced actions than during the observation of practiced actions in novices [2,39]. This finding suggests that the MNS plays a useful role in the early stages of motor learning, which supports the present findings for novices; i.e., observation combined with MI of a non-practiced skilled hand-motor task effectively increased cortical excitability in the novices.

When we try to learn a difficult and skilled motor task, we usually observe, imagine, and imitate the task being performed well by another person. The present results provide experimental evidence for the efficacy of this approach. In particular, the finding that observation combined with MI of a task effectively enhances motor cortical excitability in novices. It suggests the utility of practical motor skill training involving the presentation of a model action combined with MI. This practical approach could be an efficient motor skill learning method. Acknowledgment This study was supported in part by a Grant-in-Aid from the Ministry of Education, Culture, Sports, Science, and Technology of Japan (Grant no. 21500630).

References

- [1] G. Abbruzzese, C. Trompetto, M. Schieppati, The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. Exp. Brain Res. 111 (1996) 465–472.
- [2] G. Buccino, S. Vogt, A. Ritzl, G.R. Fink, K. Zilles, H.J. Freund, G. Rizzolatti, Neural circuits underlying imitation learning of hand actions; an event related fMRI study. Neuron 42 (2004) 323–334.
- [3] R.S. Burhans, C.L. Richman, D.B. Bergey, Mental imagery training: effects on running speed performance. Int. J. Sport Psychol. 19 (1998) 26–31.
- [4] B. Calvo-Merino, D.E. Glaser, J. Grèzes, R.E. Passingham, P. Haggard, Action observation and acquired motor skills: an FMRI study with expert dancers. Cereb. Cortex 15 (2005) 1243–1249.
- [5] B. Calvo-Merino, J. Grèzes, D.E. Glaser, R.E. Passingham, P. Haggard, Seeing or doing? Influence of visual and motor familiarity in action observation. Curr. Biol. 16 (2006) 1905–1910.
- [6] J.W. Carolee, S.T. Grafton, P.S. Pohl, Motor task difficulty and brain activity: investigation of goal-directed reciprocal aiming using positron emission tomography. J. Neurophysiol. 77 (1997) 1581-1594.
- [7] J. Decety, J. Grèzes, Nerual mechaisms subserving the perception of human

actions. Trends Cogn. Sci. 3 (1999) 172-178.

- [8] H.H. Ehrsson, A. Fagergren, T. Jonsson, G. Westling, R.S. Johansson, H. Forssberg, Cortical activity in precision-versus powergrip tasks: an fMRI study. J. Neurophysiol. 83 (2000) 528–536.
- [9] H.H. Ehrsson, E. Fagergren, H. Forssberg, Differential frontoparietal activation depending on force used in a precision grip task: an fMRI study. J. Neurophysiol. 85 (2001) 2613–2623.
- [10] L. Fadiga, L. Fogassi, G. Pavesi, G. Rizzolatti, Motor facilitation during action observation: a magnetic stimulation study. J. Neurophysiol. 73 (1995) 2608–2611.
- [11] L. Fadiga, G. Buccino, L. Craighero, L. Fogassi, V. Gallese, G. Pavesi, Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. Neuropsychol. 37 (1999) 147-158.
- [12] A.D. Fourkas, A. Avenanti, C. Urgesi, S.M. Aglioti, Corticospinal facilitation during first and third person imagery. Exp. Brain Res. 168 (2006) 143–151.
- [13] S.T. Grafton, M. A. Arbib, L. Fadiga, G. Rizzolatti, Localization of grasp representations in humans by positron emission tomography. 2. observation compared with imagination. Exp. Brain Res. 112 (1996a) 103–111.
- [14] S.T. Grafton, A.H. Fagg, R.P. Woods, M.A. Arbib, Functional anatomy of pointing

and grasping in humans. Cereb. Cortex 6 (1996b) 226-237.

- [15] J. Grèzes, J. Decety, Functional anatomy of execution, metal simulation, observation, and verb generation of actions: a meta-analysis. Hum. Brain Mapp. 12 (2001) 1-19.
- [16] R. Hashimoto, J.C. Rothwell, Dynamic changes in corticospinal excitability during motor imagery. Exp. Brain Res. 125 (1999) 75–81.
- [17] K. Hashizume, Y. Matsuo, Temporal and spatial factors reflecting performance improvement during learning three-ball cascade juggling. Hum. Mov. Sci. 23 (2004) 207-233.
- [18] B.L. Howe, Imagery and sport performance. Sports Med. 11 (1991) 1-5.
- [19] M. Jeannerod, Neural simulation of action: a unifying mechanism for motor cognition. NeuroImage 14 (2001) 103–109.
- [20] T. Kasai, S. Kawai, M. Kawanishi, S. Yahagi, Evidence for facilitation of motor evoked potentials (MEPs) induced by motor imagery. Brain Res. 744 (1997) 147–150.
- [21] H. Kinoshita, N. Oku, K. Hashikawa, T. Nishimura, Functional brain areas used for the lifting of objects using a precision grip: a PET study. Brain Res. 857 (2000) 119–130.

- [22] F. Maeda, G. Kleiner-Fisman, A. Pascual-Leone, Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation.
 J. Neurophysiol. 87 (2002) 1329–1335.
- [23] R.C. Miall, D.M. Wolpert, Forward models for physiological motor control. Neural Networks 9 (1996) 1265-1279.
- [24] N. Nishitani, R. Hari, Temporal dynamics of cortical representation for action.Proc. Natl. Acad. Sci. USA. 97 (2000) 913-918.
- [25] N. Nishitani, R. Hari, Viewing lip forms: cortical dynamics. Neuron 36 (2002) 1211-1220.
- [26] R. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychol. 9 (1971) 97–113.
- [27] A. Pascual-Leone, J. Grafman, M. Hallett, Modulation of cortical motor output maps during development of implicit and explicit knowledge. Science 263 (1994) 1287-1289.
- [28] A. Pascual-Leone, N. Dang, L.G. Cohen, J.P. Brasil-Neto, A. Cammarota, M. Hallett, Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. J. Neurophysiol. 74 (1995) 1037-1045.

- [29] G. Rizzolatti, L. Fadiga, M. Matelli, V. Bettinardi, E. Paulesu, D. Perani, F. Fazio, Localization of grasp representations in humans by PET. I. Observation versus execution. Exp. Brain Res. 111 (1996) 246–252.
- [30] M. Roosink, I. Zijdewind, Corticospinal excitability during observation and imagery of simple and complex hand tasks: implication for motor rehabilitation. Behav Brain Res 213 (2010) 35-41.
- [31] P.M. Rossini, S. Rossi, P. Pasqualetti, F. Tecchio, Corticospinal exitability modulation to hand muscles during movement imagery. Cereb. Cortex 9 (1999) 161-167.
- [32] B.S. Rushall, L.G. Lippman, The role of imagery in physical performance. Int. J.Sport Psychol. 29 (1997) 57-72.
- [33] M. Sakamoto, T. Muraoka, N. Mizuguchi, K. Kaosue, Combining observation and imagery of an action enhances human corticospinal excitability. Neurosci. Res. 65 (2009) 23-27.
- [34] K. Stefan, L.G. Cohen, J. Duque, R. Mazzocchio, P. Celnik, L. Sawaki, L. Ungerleider, J. Classen, Formation of a motor memory by action observation. J. Neurosci. 25 (2005) 9339-9346.
- [35] K. Stefan, J. Classen, P. Celink, L.G. Cohen, Concurrent action observation

modulates practice-induced motor memory formation. Eur. J. Neurosci. 27 (2008) 730-738.

- [36] A.P. Strafella, T. Paus, Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. Neuroreport 11 (2000) 2289-2292.
- [37] H. Tsuda, T. Aoki, N. Oku, Y. Kimura, J. Hatazawa, H. Kinoshita, Functional Brain Areas associated with manipulation of a prehensile tool: a PET study. Hum. Brain Mapp. 30 (2009) 2879-2889.
- [38] M.A. Umilta, E. Kohler, V. Gallese, L. Fogassi, L. Fadiga, C. Keysers, G. Rizzolatti, I know what you are doing: a neurophysiological study. Neuron 31 (2001) 155-165.
- [39] A. Vogt, G. Buccino, A.M. Wohlschager, N. Canessa, N.J. Shah, K. Zilles, S.B. Eickhoff, H.J. Freund, G. Rizzolatti, G.R. Fink, Prefrontal involvement in imitation learning of hand actions: Effect of practice and Expertise. NeuroImage 37 (2007) 1371-1383.
- [40] D.M. Wolpert, Z. Ghahramani, M.I. Jordan, An internal model for sensorimotor integration. Science 269 (1995) 1880–1882.
- [41] D.M. Wolpert, J.R. Flanagan, Motor prediction. Curr. Biol. 11 (2001) 729–732.

[42] S. Yahagi, T. Kasai, Facilitation of motor evoked potentials (MEPs) in first dorsal interosseous (FDI) muscle is dependent on different motor images.
 Electroencephalogr. Clinic. Neurophysiol. 109 (1998) 409–417.

Figure legends

Fig. 1. Frames from video clips of the 3BCJ and p3BCJ.

Fig. 2. Mean VAS scores (mm; \pm SD) measured in each MI condition in the novices and experts. *p<0.01.

Fig. 3. Mean MEP amplitude (% of control; \pm SD) recorded in the FDI, APB, and ADM in each experimental condition in the novices (A) and experts (B). A horisontal broken line shows baseline control. *p<0.01.

A frame from a video clip of 3BCJ



A frame from a video clip of p3BCJ





Fig.3

