

In the Here and Now.
**Enhanced motor corticospinal excitability in novices when
watching live compared to video recorded dance**

Corinne Jola¹ and Marie-Hélène Grosbras²

¹NeuroSpin Center, CEA, Gif-sur-Yvette, France

²Institute of Neuroscience and Psychology, University of Glasgow, UK

Short title: Live versus video: Motor corticospinal excitability

Corresponding Author:

Dr C Jola

NeuroSpin Center

Commissariat à l'Énergie Atomique

Département des Sciences de la Vie/Institute d'Imagerie Biomédicale

91191 Gif-sur-Yvette

France

Corinne.JOLA@cea.fr

Abstract/Summary

Enhanced motor corticospinal excitability (MCE) in passive action observation is thought to signify covert motor resonance with the actions seen. Actions performed by others are an important social stimulus and thus, motor resonance is prevalent during social interaction. However, most studies employ simple/short snippets of recorded movements devoid of any real-life social context, which has recently been criticized for lacking ecological validity. Here, we investigated whether the co-presence of the actor and the spectator has an impact on motor resonance by comparing novices' MCE for the finger (FDI) and the arm (ECR) with single-pulse transcranial magnetic stimulation when watching 5-minute solos of ballet dance, Indian dance and an acting control condition either live or on video. We found that (1) MCE measured in the arm muscle was significantly enhanced in the live compared to the video condition, (2) differences across performances were only evident in the live condition, and (3) our novices reported enjoying the live presentations significantly more. We suggest that novice spectators' MCE is susceptible to the performers' live presence.

Keywords: corticospinal excitability – action observation – novices – mirror neuron – performance – live presence

Acknowledgments

This research was funded by the AHRC (www.watchingdance.org) and we thank our project collaborators for their helpful comments on a previous version of this manuscript. Data collection was supported by David Stroud and Susan Beaton. We especially thank the Scottish Ballet, in particular Charlotte Gross, the dance expert Seon Hee Jang (ballet) and our performers Kimberley Lawrie, Annapoorna Kuppuswamy and Catherine Hoffmann.

Introduction

It has been suggested that onlookers covertly simulate movements they observe (Jeannerod, 1994), which may help understand the meaning of the actions as part of the mirror neuron activity (e.g. Gallese, Keysers, & Rizzolatti, 2004; Rizzolatti & Sinigaglia, 2010). Thus, when spectators ‘resonate’ with observed actions, the motor system of the spectator automatically simulates the models’ actions internally (e.g., Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995), allowing purposeful social interactions.

Many studies have reported enhanced cortical activity during action observation when the observed actions matched the spectator’s motor repertoire (for an overview, see Bläsing et al., 2012; Sevdalis & Keller, 2011). Also, using live, professionally performed solos of extended duration (5 minutes), we found enhanced muscle-specific motor simulation in spectators with visual but no motor expertise (Jola, Abedian-Amiri, Kuppuswamy, Pollick, & Grosbras, 2012). Indeed, partial evidence indicates that observing live and digitally mediated actions modulates motor cortex activity differently in both adults and children (Järveläinen, Schürmann, Avikainen, & Hari, 2001; Shimada & Hiraki, 2006). However, so far, the effect of the stimulus presentation on adult motor resonance mechanisms has widely been neglected. The need for further systematic investigations of the role of ecological validity in studying the brain’s activity during components of social interaction – such as observing others’ actions – has been voiced more recently (see Risko, Laidlaw, Freeth, Foulsham, & Kingstone, 2012).

Here, we empirically compared novices' neurophysiological responses to watching dance live versus on video. Importantly, none of the participants had visual or physical experience of the actions observed. This allowed to measure whether the co-presence of the performer and the spectator, i.e. the 'liveness' (Auslander, 2008), has a measurable impact on action observation processes (separate from the potential factor of expertise). We stimulated the primary motor cortex with single-pulse transcranial magnetic stimulation (TMS) under different viewing conditions, while recording the muscular response with electromyography (EMG, Abbruzzese & Trompetto, 2002; Chen, 2000). Larger motor evoked potentials (MEPs) indicate higher excitability of the corticospinal tract (Petersen, Pyndt, & Nielsen, 2003) at the moment of stimulation. This is taken as an index of motor cortex activity engaged during simulation (Fadiga, Craighero, & Olivier, 2005) of specific muscle groups (Alaerts, Swinnen, & Wenderoth, 2009; Strafella & Paus, 2000). With this method, motor activity during action observation has been found to be modulated by motor as well as visual expertise (Aglioti, Cesari, Romani, & Urgesi, 2008; Jola, Abedian-Amiri et al., 2012), expanding previous knowledge of enhanced brain activity in physically trained spectators as found through other neuroscientific techniques, such as functional Magnetic Resonance Imaging (e.g., Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005; Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006).

No study has yet investigated how visual exposure affects the muscle-specific motor activity differently during action observation depending on whether the action is presented live (i.e., when both performer and spectator are both physically present in the same place at the same time and share the experience in the moment), or recorded (i.e.,

when there is a temporal gap between production and perception, see Auslander, 2008). We thus investigated muscle-specific MCE of novices in response to two presentation forms (live vs. video) for two globally established narrative dance forms (ballet and Bharatanatyam, a classical Indian dance), which use the hands and fingers in very different ways: in ballet, the extensor of the arm (extensor carpi radialis, ECR) is significantly more activated than the index finger flexor (first dorsal interosus, FDI); whereas the fingers are more important in Bharatanatyam (Jola, Abedian-Amiri et al., 2012). We expected watching others' actions live to enhance MCE, as indicated by larger MEP amplitudes for actions viewed live compared to on video. Additionally, participants' levels of enjoyment of watching the performances were assessed to control for effects of activation that could be linked to how participants subjectively relate to the observed movements.

Material and Methods

Participants

The 20 participants included in the study (age 20-45 years, MEAN±SD: 25.65±7.99, 10 female) were recruited via the University of Glasgow School of Psychology and screened for dancing experience as well as contra-indication to TMS. Of these, 11 watched the performances on video (age: 21.55±0.82, 54.55 % female) and 9 live (age: 30.67±9.96, 44.45 % female). The distribution of age and gender did not differ significantly across the two groups, Mann-Whitney U Test, $p = 0.113$ (age); $p = 0.661$ (gender). All were Caucasian and novices regarding dance, with no formal dance training

and no experience in watching professional staged ballet or Bharatanatyam. Participants who saw the performances live were included in another separate study published elsewhere (Jola, Abedian-Amiri et al., 2012). Both studies were approved by the local ethics committee (FIMS0522). All participants gave written informed consent and received financial compensation.

Conditions

Participants' MCE was measured in three within-subjects viewing conditions; by means of 30 single pulses delivered during three types of solo performances (ballet, Bharatanatyam, and acting) each lasting five minutes. Further, we measured MCE at rest (eyes closed) before (30 single pulses) and after (15 single pulses) each performance. The between-subjects factor was presentation form, with one group of participants being exposed to the live performances and the other to a video recording of the performances.

The performances were staged by professional female performers to recorded music. The ballet was a concatenation of fairy solos from the *Sleeping Beauty* with the corresponding music extracts. The Bharatanatyam was a traditional Indian dance piece performed with traditional music. A specially commissioned acting performance was specifically designed to match the use of the space and bodily actions (clapping, stamping, and making a fist) of the two dance pieces; accompanied by instrumental background music. The order of the performances was counterbalanced. Importantly, the dance styles differed in the use of the arm and hand muscle groups. At the specific time-points of stimulation, ballet employed movements that required contraction of ECR significantly more often than FDI muscle groups; whereas for the Bharatanatyam it was

significantly more often FDI than ECR induced movements (see Jola Abedian-Amiri et al., 2012). Further, the use of gestures (short actions of miming character that contain a specific meaning) differed between the performances. The Bharatanatyam used here was a popular 'padam' which is the form that uses most gestural expressions of the classical Indian dance repertoire. We asked a separate sample of five participants that did not participate in the TMS experiment to watch each video and note the number of gestural actions they spot in the performances – independent on whether they actually understand the gesture or not. For each participant, the number of gestures perceived in ballet, Bharatanatyam and the acting performance was computed as a ratio of the individual overall counted gestures. As expected, participants saw significantly more gestures in the Bharatanatyam performance ($55.93\% \pm 11.17$) than either during the ballet ($24.12\% \pm 5.69$) or acting ($19.94\% \pm 10.40$), $t(4) = 4.95$, $p = 0.008$ (Ballet vs. Bharatanatyam), $t(4) = 3.86$, $p = 0.018$ (Acting vs. Bharatanatyam), but $t(4) = 0.75$, $p = 0.496$ (Ballet vs. Acting). Thus, Bharatanatyam contains significantly more gestural actions than the other performances.

Each performance was presented either live or in the form of a straight unedited recording on a computer screen (Fig. 1). Each live performance was recorded in the background during the testing (for experimental documentation and post-hoc analysis). The digital versions were recorded during a separate session without any experimental subject spectators but on the same day and in the same space of the live testing in order to have a matching visual background in the two conditions live and video. The performances for the recording conditions were filmed in digital format with a wide angle lens in HDV 1080i Standard (Sony XDCAM). In the video conditions, participants

passively watched the videos with a viewing angle of 19.1° on a 17'' analogue CRT computer screen set to 85Hz and a resolution of 1024x768. The viewing angle of the live performance had a range of 6.04° to 80.73° since the performers moved in depth. Importantly, the minimum visual angle in both presentation conditions was still larger than the human focal vision. All three performances and the experimental space are described in further detail in Jola, Abedian-Amiri et al. (2012) and can be viewed online (<http://paco.psy.gla.ac.uk/watchingdance>).

Questionnaires

After testing, participants filled out a questionnaire regarding their experience in dance and other physical activities as well as their level of enjoyment of the performances seen (all on 10-point Likert scales).

TMS/EMG

Single-TMS monophasic pulses were delivered using a Magstim 200 stimulator (Dyfed, UK) according to standard procedure (e.g., Wassermann et al., 2008). We used a 90 mm circular coil with anticlockwise current flow, and positioned its center over the vertex, such that the edge of the coil, where the magnetic field is produced, covered the middle upper part of the central sulcus. We could thereby elicit MEPs simultaneously in both the right extensor carpi radialis (ECR) in the forearm and the right first dorsal interosseous (FDI) in the hand. TMS intensity was set at 120% of the resting motor threshold. The threshold was defined for each participant individually as the lowest TMS intensity that elicited MEPs in the FDI muscle larger than $50 \mu\text{V}$ in 5 out of 10 stimulations. This threshold was distributed equally in the two groups (mean percent of

maximal stimulator output: live 53.11 ± 6.39 (SD) and video 47.00 ± 4.94 , Mann-Whitney U test $p = 0.092$. EMG responses of the ECR and FDI were detected by 8 mm Ag/AgCl sintered flat electrodes in a standard belly-tendon montage. The ground electrode was placed at the elbow joint. EMG baseline corrected signals were recorded in time-windows of 500 ms using a customized pre-amplifier (CED 1902) and software (Signal 4.06) at a gain of 1000 x, 2.5 kHz sampling rate, 20-1000 Hz filter and Notch Filter.

Testing Procedure

Participants who were shown the video were tested individually in a dedicated testing space. They rested their head on a chin rest and the movements of the TMS coil were tracked using Brainsight (Rogue research) (Fig. 1, left). The other participants saw the live performance in the rehearsal space of the Scottish Ballet (Fig. 1, right). In order to minimize the number of live performance runs two participants watched each performance at the same time (with an occluding panel between them), receiving TMS at the same time points. Participants were asked to wear ear protection, but were still able to hear the music that accompanied the dance performances. Participants were invited to simply enjoy the performances they were going to watch. The TMS coils were held in place by four different experimenters, of whom two tested the participants in both presentation forms. TMS pulses were triggered with a random jitter and were a minimum of 5 seconds and a maximum of 9 seconds apart.

Data Analysis

After visual inspection, all MEP amplitudes (from min peak to max peak within a time-window of 10 to 50 ms after the TMS trigger) were included in the analysis, using a

dedicated Matlab script (Mathworks, Inc, 2008). To test for effects of presentation, we calculated MEPs percentage changes to baseline. Main and interaction effects were tested using mixed-model univariate approach to repeated-measures ANOVA in SPSS 18 with the between-subjects factor presentation live (N = 11) vs. video (N = 9) and the within-subjects factor performance (ballet, Bharatanatyam, acting). Since the size of our groups was unbalanced, type III sum of squares method was used. Based on previous findings (Jola, Abedian-Amiri et al., 2012), we included age as a covariate in the MEP analyses.

Results

1. MEP changes throughout the experiment

TMS itself did not induce a change in MCE over the time course of the experiment. MEPs average amplitude of the two rest conditions (before vs. after stimulation) across all three performances did not show any significant modulation. The mixed-design ANOVA showed neither for FDI nor ECR a significant main or interaction effect on presentation form or rest condition (all $p > 0.4$). The two rest conditions (before and after each performance) were thus averaged to one baseline.

2. Effect of Presentation (video vs. live) on Action Observation

The mixed-design ANOVA on MEP percentage changes from the baseline showed a significant interaction between presentation and performance in both muscles, FDI: $F(2, 34) = 4.71, p = 0.016$; and ECR: $F(2, 34) = 3.29, p = 0.049$. Moreover, in ECR, the factor presentation revealed a significant main effect, reflecting higher mean MEP percentage changes in the live compared to the video condition, $F(1, 17) = 6.25, p =$

0.023, Mean±SE: 59.74±11.70 (live) vs. 16.87±10.37 (video). However, FDI MEP percentage changes did not show a significant main effect of presentation, $F(1, 17) = 0.002, p = 0.969, 35.25±16.97$ (live) vs. $34.28±15.03$ (video). Performance type was not a significant main factor in ECR, $F(2, 34) = 1.39, p = 0.262, 34.21±7.59$ (ballet), $50.13±12.97$ (Bharatanatyam), and $30.59±7.91$ (acting), but was in FDI, $F(2, 34) = 3.73, p = 0.034, 28.99±11.10$ (ballet), $42.13±14.63$ (Indian dance), and $33.19±12.10$ (acting). The same mixed-design ANOVA for the live and video condition run separately revealed significant linear effects for MEPs during ballet, acting, and Bharatanatyam in both muscles in the live but not the video condition, ECR: $F(1, 7) = 5.75, p = 0.048$ (live), $F(1, 9) = 0.01, p = 0.926$ (video), FDI: $F(1, 7) = 6.732, p = 0.036$ (live), and $F(1, 9) = 0.82, p = 0.389$ (video). Post-hoc paired samples *t*-tests (Fig. 2, bottom) showed significantly larger ECR MEP amplitudes in the live condition when novices watched the Bharatanatyam compared to either ballet or acting, $t(8) = 2.50, p = 0.037$ (Bharatanatyam-ballet); $t(8) = 2.62, p = 0.031$ (Bharatanatyam-acting). Further, independent *t*-tests showed a trend for larger percentage changes when Bharatanatyam was viewed live compared to video, $t(18) = 1.15, p = 0.089$. No simple contrast in FDI reached significance (Fig. 2, top), however a trend for larger differences between ballet and Bharatanatyam for live compared to video presentations was observed, $t(18) = 2.08, p = 0.052$.

-----Insert Figure 2 about here -----

3) *Enjoyment*

The mixed-design ANOVA on enjoyment ratings showed a significant interaction of presentation and performance, $F(2, 36) = 8.57, p = 0.001$, and main effects of

presentation, $F(1, 18) = 6.89, p = 0.017$, and performance $F(2, 36) = 17.12, p < 0.001$. Overall, performances were enjoyed more when watched live than on video, Mean \pm SD: 5.33 \pm 1.46 (live) vs. 3.69 \pm 1.15 (video). Specifically, significantly higher enjoyment ratings were given when participants watched the acting as well as Bharatanatyam live compared to on video, $t(18) = 2.29, p = 0.035$ (acting), $t(9.42) = 4.41, p = 0.002$ (Bharatanatyam, corrected for unequal variances). Ballet, Bharatanatyam, and acting were enjoyed equally (Fig. 3) when viewed live, $F(2, 16) = 1.87, p = 0.187$. However, when viewed on video, enjoyment ratings between the performances differed significantly, $F(2, 20) = 21.66, p < 0.001$. On video, both ballet and Bharatanatyam were enjoyed significantly more than the acting, $t(10) = 5.78, p < 0.001$ (ballet-acting), and $t(10) = 5.18, p = 0.001$ (Bharatanatyam-acting) and ballet was enjoyed significantly more than Bharatanatyam, $t(10) = 2.51, p = 0.031$ (ballet-Bharatanatyam).

-----Insert Figure 3 about here -----

General Discussion

We investigated if live compared to video presentation of solo performances (ballet, Bharatanatyam, acting) affected MCE of novices. Firstly, we found higher MCE in the arm muscle groups (ECR) when performances were watched live compared to on video. Secondly, levels of MCE were modulated by the performance type in the live setting only, with largest MEPs in the Bharatanatyam compared to ballet or acting, particularly in the arm muscle. Further, the performances were enjoyed more when watched live compare to on video. Finally, while levels of enjoyment were unaffected by the performance type in the live presentation, they differed in the video condition.

Hence, live performances evoked stronger covert motor simulation in novice spectators than presentations on video, and they were also enjoyed more. Notably, action observation processes could be influenced by how much a dance movement is appreciated (e.g., Calvo-Merino, Jola, Glaser, & Haggard, 2008; Cross, Kirsch, Ticini, & Schütz-Bosbach, 2011). However, there was no direct relationship between enjoyment ratings and audiences' indices of motor simulation: First, our performances (ballet, Bharatanatyam or acting) were distinctly liked or disliked in the video condition, whereas we found no significant difference between MCE of individual performances in the video condition. Second, in the live condition, the dance performances were equally enjoyed whilst MCE was selectively modulated. Our findings are in line with the reported dissociation between action and object-motion observation in children in live but not TV settings by Shimada and Hiraki (2006). Such difference could be related to the notion of presence, the co-presence of the performer and spectator. In most psychological experiments, however, presence has not been fully investigated as a potential modifier of neuro-functional relevance, although Electroencephalography (e.g., Pönkänen, Alhoniemi, Leppänen, Hietanen, 2011) and fMRI (Redcay et al., 2010) studies suggests that live stimuli amplify brain activity components associated with the perception of signals with high affective or motivational relevance. As MCE was previously found to be influenced by affective stimulus components (e.g., Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2006; Coelho, Lipp, Marinovic, Wallis, & Riek, 2010; but see also Borgomaneri, Gazzola, & Avenanti, 2012), it is possible, that the enhanced MCE is a response to higher affective or motivational relevance of live compared to video stimuli.

We used the measure of enjoyment to capture whether effects of activation were linked to how participants subjectively related to the observed movements. Although our study does not allow dissociating motor from affective components and it thus remains uncertain whether modulation of MCE reflects purely motor simulation or not, the different patterns for the objective (MCE) and subjective measures (ratings) suggest that they reflect, at least partly, different phenomena. Thus, while mediated environments may present an exceptional experimental tool for conducting social psychological research (Loomis, Blascovich, & Beall, 1999), our results suggest that further investigations are required to exclude potential effects of experiencing natural, so-called 1st order versus technology mediated or 2nd order presence (ISPR, 2000).

One important difference between the viewing conditions is the size of the stimuli. It could be argued, that the visual angle for arm movements on the video was smaller and thus they were less imminent than in the live performance. This is, however, not always the case as in the live performance; the visual angle was dependent on the spatial location of the performer, and thus sometimes viewed from a further distance. The perception of face and gaze cues, whose processing is influenced by the distance (e.g. Gale, Spratt, Chapman, & Smallbone, 1975), could also have influenced action observation mechanisms, although in that case we might have expected significant differences between the individual performances in both of the measured muscles. Importantly, novices' as well as experts' eye fixations when watching a dance routine on video were found to be located more on the background than the dancer (Stevens et al., 2010). To complete our understanding of how the presentation form of the stimuli affect motor mapping in action observation, further studies are needed to compare eye fixations

in live performances and video performances, with particular reference to distance and face cues.

We observed the highest MCE for Bharatanatyam in the live condition and in the arm muscle. Notably, the Bharatanatyam used here contained significantly more gestures than the ballet or the acting performance (see methods). However, as the finger movements in the Bharatanatyam are hugely relevant but difficult to perform, we suggest that novice spectators may have responded on the level of their physical capabilities (ECR only) rather than on a complete motor matching of the performers' actions (ECR and FDI). Also one has to consider the specificity of studying dance (e.g., Cross & Ticini, 2012; Jola, Ehrenberg, & Reynolds, 2012). The dance styles differ in a number of dimensions, including the range of movements, degree of abstraction and soundscape. Since dance performances combine several of these so-called 'strands' to transmit a sense of motion to the audience, we chose to keep the full dimensionality. In studying the effects of 'liveness' it was important to present dance in an ecologically valid form and not to reduce the stimuli to one aspect of the dance only. Moreover, ballet is more prevalent in western culture than Indian dance. Our novice spectators may thus have a certain level of familiarity with some elements of ballet. However, without specific exposure to ballet performances, novices remain unfamiliar with the classical form of ballet (Jola, Abedian-Amiri et al., 2012; Reason & Reynolds, 2010) that includes all its strands (as they would then be defined by us as experts).

For the first time, we thus show evidence of performance-sensitive but not muscle-specific MCE to novel gestures of the arm when the whole body is presented live.

Previous studies, using video stimuli, reported enhanced motor resonance when experts observe familiar compared to unfamiliar movements over and above the activity of novices. We think that in our study the presence of the performer evoked performance (content) specific covert simulation even in novices. We thus suggest two potentially different processes for enhanced MCE as reported recently by others for mirror neuron mechanism (e.g., Silas, Levy, & Holmes, 2012). We first propose a response composed of purely resonance characteristics with the observed movements, where the spectators' motor resonance does not fully match with the motor properties of the observed actions. This is also in line with recent studies that found enhanced premotor cortex activity when children watched motion patterns that were neither familiar nor executable (e.g., Grossmann, Cross, Ticini, & Daum, 2012; Virji-Babul, Rose, Moiseeva, & Makan, 2012). Further, if an action cannot be executed, it cannot be simulated as such and thus such a general resonance contradicts conventional views of automatic motor simulation as a support mechanism for action understanding. For this processes to appear, either an engaging environment such as live presentations (as used here), stimuli valence (e.g., Enticott et al., 2012, but see also Borgomaneri et al., 2012), visual experience (Jola, Abedian-Amiri et al., 2012) or an imitation task (Hardwick, McAllister, Holmes, & Edwards, 2012) is necessary. Then, in order to evoke an embodied simulation that is fully matching the motor properties of the observed action, physical expertise is required (e.g., Aglioti et al., 2008).

Familiar stimuli are inherently relevant to expert viewers and motor equivalence in covert simulation can be assumed to be of greater functional importance than non-equivalence. We therefore suggest that the two processes described above (the general

response to actions with purely resonance characteristics and the muscle specific response to the actions) are sequential in that order. Further studies are required to test the validity of this two-stage model.

Restrictions on observers' actions, such as by tying their hands, have been found to interfere with simulation during action observation, as inferred by spectators' proactive gaze behavior (see Ambrosini, Sinigaglia, Costantini, 2012). Our participants in the video condition had their head positioned in a chin rest and were thus less free to move than the participants in the live condition. We think, however, it is unlikely that the restrained head impacted significantly upon MEPs in the hands and arms (which were unrestrained in both conditions). All participants of both presentation conditions stated they felt comfortable with the measurement environment. Notably, we not only found significant MEP differences between presentation forms but also between dance conditions. Nevertheless, as in all previous TMS studies, participants were asked to keep their head and measured muscle groups still. Future studies should test the effects of free-viewing and restricted viewing as one aspect of ecological validity.

Our findings are important in view of the existing literature on action observation, which commonly uses video as the presentation form of choice. The results from this first step into studying MCE in complex real-live settings suggest four arguments for using live rather than video presentations for social stimuli such as dance: (1) higher MCE in the arm, (2) performance-specific MCE, (3) higher levels of enjoyment, and (4) no significant differences in enjoyment ratings across performance types. Further support of our findings will benefit therapy and research as both increasingly use computerized representation rather than live presentation.

References

- Abbruzzese, G., & Trompetto, C. (2002). Clinical and research methods for evaluating cortical excitability. *Journal of Clinical Neurophysiology*, *19*, 307–321.
- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, *11*, 1109-1116.
- Alaerts, K., Swinnen, S. P., & Wenderoth, N. (2009). Is the human primary motor cortex activated by muscular or direction-dependent features of observed movements? *Cortex*, *45*, 1148-1155.
- Ambrosini, E., Sinigaglia, C., Costantini, M. (2012). Tie my hands, tie my eyes. *Journal of Experimental Psychology. Human Perception and Performance*, *38*, 263-266.
- Auslander, Ph. (2008). *Liveness. Performance in a mediatized culture*. 2nd Ed. Routledge: London.
- Avenanti, A., Minio-Paluello, I., Bufalari, I., Aglioti, S.M. (2006). Stimulus-driven modulation of motor-evoked potentials during observation of others' pain. *Neuroimage*, *32*, 316-324.
- Bläsing, B., Calvo-Merino, B., Cross, E., Jola, C., Honisch, J., & Stevens, C. (2012). Neurocognitive control in dance perception and performance. *Acta Psychologica*, *139*, 300-308.
- Borgomaneri, S., Gazzola, V., Avenanti, A. (2012). Motor mapping of implied actions during perception of emotional body language. *Brain Stimulaton*, *5*, 70-76.
- Calvo-Merino, B., Glaser, D.E., Grèzes, J., Passingham, R. E., & Haggard, P. (2005). Action observation and acquired motor skills: an fMRI study with expert dancers. *Cerebral Cortex*, *15*, 1243-1249.

- Calvo-Merino, B., Grèzes, J., Glaser, D. E., Passingham, R. E., & Haggard, P. (2006). Seeing or doing? Influence of visual and motor familiarity in action observation. *Current Biology*, *16*, 1905-1910.
- Calvo-Merino, B., Jola, C., Glaser, D. E., & Haggard, P. (2008). Towards a sensorimotor aesthetics of performing art. *Consciousness and Cognition*, *17*, 911-922.
- Chen, R. (2000). Studies of human motor physiology with transcranial magnetic stimulation. *Muscle Nerve Supplement*, *9*, S26-32.
- Coelho, C. M., Lipp, O.V., Marinovic, W., Wallis, G., Riek, S. (2010). Increased corticospinal excitability induced by unpleasant visual stimuli. *Neuroscience Letters*, *481*, 135-138.
- Cross, E. S., Kirsch, L., Ticini, L. F., & Schütz-Bosbach, S. (2011). The impact of aesthetic evaluation and physical ability on dance perception. *Frontiers in Human Neuroscience*, *5*, 102.
- Cross, E. S., & Ticini, L. F. (2012). Neuroaesthetics and beyond: new horizons in applying the science of the brain to the art of dance. *Phenomenology and the Cognitive Sciences*, *11*, 5-16.
- Enticott, P. G., Harrison, B.A., Arnold, S. L., Nibaldi, K., Segrave, R. A., Fitzgibbon, B. M., Kennedy, H.A., Lau, K., & Fitzgerald, P. B. (2012). Emotional valence modulates putative mirror neuron activity. *Neuroscience Letters*, *508*, 56-59.
- Fadiga, L., Craighero, L., Olivier, E. (2005). Human motor cortex excitability during the perception of others' action. *Current Opinion in Neurobiology*, *15*, 213-218.
- Fadiga, L., Fogassi, L., Pavesi, G., & Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology*, *73*, 2608-2611.

- Gale, A., Spratt, G., Chapman, A. J., & Smallbone, A. (1975). EEG correlates of eye contact and interpersonal distance. *Biological Psychology*, *3*, 237-245.
- Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*, 396-403.
- Grossmann, T., Cross, E.S., Ticini, L. F., Daum, M. M. (2012). Action observation in the infant brain: The role of body form and motion. *Social Neuroscience, iFirst*, *13*, 1–9.
- Hardwick, R. M., McAllister, C. J., Holmes, P. S., & Edwards, M. G. (2012). Transcranial magnetic stimulation reveals modulation of corticospinal excitability when observing actions with the intention to imitate. *European Journal of Neuroscience*, *35*, 1475-1480.
- ISPR / International Society for Presence Research. (2000). The Concept of Presence: Explication Statement. Retrieved 23rd March, 2012, from <http://ispr.info/>.
- Järveläinen, J., Schürmann, M., Avikainen, S., & Hari, R. (2001). Stronger reactivity of the human primary motor cortex during observation of live rather than video motor acts. *NeuroReport*, *12*, 3493-3495.
- Jeannerod, M. (1994). The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, *17*, 187-245.
- Jola, C., Abedian-Amiri, A., Kuppaswamy, A., Pollick, F. E., & Grosbras, M. H. (2012). Motor simulation without motor expertise: enhanced corticospinal excitability in visually experienced dance spectators. *PLoS ONE*, *7*, e33343.
- Jola, C., Ehrenberg, S., Reynolds, D. (2012). The experience of watching dance: phenomenological-neuroscience duets. *Phenomenology and the Cognitive Sciences*, *11*, 17-37.

- Loomis, J. M., Blascovich, J. J., & Beall, A. C. (1999). Immersive virtual environment technology as a basic research tool in psychology. *Behavior Research Methods, Instruments, & Computers, 31*, 557-564.
- Petersen, N., Pyndt, H. S., & Nielsen, J. B. (2003). Investigating human motor control by transcranial magnetic stimulation. *Experimental Brain Research, 152*, 1-16.
- Pönkänen, L. M., Alhoniemi, A., Leppänen, J. M., Hietanen, J. K. (2011). Does it make a difference if I have an eye contact with you or with your picture? An ERP study. *Social Cognitive and Affective Neurosciences, 6*, 486-494.
- Reason, M., & Reynolds, D. (2010). Kinesthesia, empathy, and related pleasures: an inquiry into audience experiences of watching dance. *Dance Research Journal, 42*, 49-75.
- Redcay, E., Dodell-Feder, D., Pearrow, M., Mavros, P., Kleiner, M., Gabrieli, J., & Saxe, R. (2010). Live face-to-face interaction during fMRI: a new tool for social cognitive neuroscience. *Neuroimage, 50*, 1639-1647.
- Risko, E. F., Laidlaw, K., Freeth, M., Foulsham, T., & Kingstone, A. (2012). Social attention with real versus reel stimuli: toward an empirical approach to concerns about ecological validity. *Front in Human Neuroscience, 6*, 143.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nature Reviews. Neuroscience, 11*, 264-74.
- Sevdalis, V., & Keller, P. E. (2011). Captured by motion: dance, action understanding, and social cognition. *Brain and Cognition, 77*, 231-236.
- Shimada, S., & Hiraki, K. (2006). Infant's brain responses to live and televised action. *NeuroImage, 32*, 930-939.

- Silas, J., Levy, J.P., & Holmes, A. (2012). Sensitivity of 'mu' rhythm modulation to the relevance of an observed movement but not to goal congruency. *International Journal of Psychophysiology*, 85, 168-173.
- Stevens, C. J., Winkler, H., Howell, C., Vidal, L.-M., Latimer, C., Milne-Home, J. (2010). Perceiving dance: schematic expectations guide experts' scanning of a contemporary dance film. *Journal of Dance Medicine and Science*, 14, 19-25.
- Strafella, A. P., & Paus, T. (2000). Modulation of cortical excitability during action observation: a transcranial magnetic stimulation study. *NeuroReport*, 11, 2289-2292.
- Virji-Babul, N., Rose, A., Moiseeva, N., & Makan, N. (2012). Neural correlates of action understanding in infants: influence of motor experience. *Brain and Behavior*, 2, 237-242.
- Wassermann, E., Epstein, Ch., Ziemann, U., Walsh, V., Paus, T., & Lisanby, S. H. (2008). Oxford Handbook of Transcranial Stimulation. Oxford University Press: Oxford.

Figure Captions

Fig. 1. Schematic representation of the experimental setup in the live condition (left) and in the video condition (right).

Fig. 2. FDI (top) and ECR (bottom) MEP percentage changes (mean and SD) to rest for ballet, Bharatanatyam and acting live (black columns) and video (grey columns) presentation forms. $*$ = $p \leq 0.05$, \dagger = $p \leq 0.10$.

Fig. 3. Subjective enjoyment ratings (mean and SD), and p -values ($***p \leq 0.001$; $**p \leq 0.01$; $*p \leq 0.05$).