

Sonification of combined action observation and motor imagery: Effects on corticospinal excitability

Fabio Castro^{a,b,*}, Paulina Anna Bryjka^c, Giovanni Di Pino^a, Aleksandra Vuckovic^d, Alexander Nowicky^e, Daniel Bishop^b

^a Research Unit of Neurophysiology and Neuroengineering of Human-Technology Interaction (Next Lab), Università Campus Bio-Medico di Roma, Rome, Italy

^b Centre for Cognitive Neuroscience, Department of Life Sciences, College of Health, Medicine and Life Sciences, Brunel University London, Uxbridge, UK

^c Department of Life Sciences, College of Health, Medicine and Life Sciences, Brunel University London, Uxbridge, UK

^d School of Engineering, College of Engineering and Science, James Watt Building (south) University of Glasgow, Glasgow G12 8QQ, UK

^e Centre for Cognitive Neuroscience, Department of Clinical Sciences, College of Health, Medicine and Life Sciences, Brunel University London, Uxbridge, UK

ARTICLE INFO

Keywords:

Transcranial magnetic stimulation
Sensory augmentation
Dual simulation hypothesis
Motor imagery
Audiomotor resonance

ABSTRACT

Action observation and motor imagery are valuable strategies for motor learning. Their simultaneous use (AOMI) increases neural activity, with related benefits for motor learning, compared to the two strategies alone. In this study, we explored how sonification influences AOMI. Twenty-five participants completed a practice block based on AOMI, motor imagery and physical execution of the same action. Participants were divided into two groups: An experimental group that practiced with sonification during AOMI (sAOMI), and a control group, which did not receive any extrinsic feedback. Corticospinal excitability at rest and during action observation and AOMI was assessed before and after practice, with and without sonification sound, to test the development of an audiomotor association. The practice block increased corticospinal excitability in all testing conditions, but sonification did not affect this. In addition, we found no differences in action observation and AOMI, irrespective of sonification. These results suggest that, at least for simple tasks, sonification of AOMI does not influence corticospinal excitability; In these conditions, sonification may have acted as a distractor. Future studies should further explore the relationship between task complexity, value of auditory information and action, to establish whether sAOMI is a valuable for motor learning.

1. Introduction

Action observation (AO) and motor imagery (MI) are two forms of action simulation which exhibit computational equivalence to physically executed actions (PE), without physical manifestation of movement (Guillot, Di Rienzo, MacIntyre, Moran, & Collet, 2012; Jeannerod, 2001, 2004). AO is thought to be a bottom-up process whereby an observed action is mapped onto the observer's own sensorimotor system (Friston, Mattout, & Kilner, 2011; Kilner, Friston, & Frith, 2007b), thus enabling action understanding (Kilner, 2011; Rizzolatti & Craighero, 2004). On the other hand, MI has been modelled as a top-down process reflecting internally-driven simulation of the efferent and afferent characteristics of the action (Kilteni, Andersson, Houborg, & Ehrsson, 2018). Thus, both AO and MI interact with the internal representation of the body and action, but from different perspectives (Vogt, Di Rienzo, Collet, Collins, & Guillot, 2013). Given the computational similarities

between simulated and executed actions, studies focussed on the use of AO and MI in motor (re)learning (Abbruzzese, Avanzino, Marchese, & Pelosin, 2015; Buccino, 2014; Mulder, 2007). Even though evidence suggests that AO and MI are suboptimal compared to PE in terms of their ability to promote motor learning (Ingram, Kraeutner, Solomon, Westwood, & Boe, 2016; Kraeutner, MacKenzie, Westwood, & Boe, 2015; Mulder, Zijlstra, Zijlstra, & Hochstenbach, 2004; Pascual-Leone et al., 1995), action simulation may represent a valuable addition to physical enactment – and in some circumstances may be the only viable alternative to physical training for rehabilitation of neurological conditions or injuries that preclude movement (Abbruzzese, Avanzino, Marchese, and Pelosin, 2015; Mulder, 2007). Under the right conditions, mental simulation training does not induce neuromuscular fatigue (Rozand, Lebon, Papaxanthis, & Lepers, 2014), making it ideal for rehabilitation and to keep sensorimotor areas active during immobilization (Bassolino, Campanella, Bove, Pozzo, & Fadiga, 2014).

* Corresponding author at: Next Lab, Via Alvaro Del Portillo, 5, 00128 Roma, Italy.
E-mail address: f.castro@unicampus.it (F. Castro).

<https://doi.org/10.1016/j.bandc.2021.105768>

Received 8 March 2021; Received in revised form 26 May 2021; Accepted 28 May 2021

Available online 16 June 2021

0278-2626/© 2021 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

One major difference between simulated and executed action is the lack of movement (Guillot et al., 2012), and consequently movement-related feedback, which is thought to be a fundamental component of motor control and learning (Ostry & Gribble, 2016; Ostry, Mattar, Wong, & Gribble, 2010). Some studies explored strategies to augment the effects of action simulation training, by pairing AO with peripheral sensory stimulation, reporting increased corticospinal excitability and improved learning, compared to non-augmented conditions (Bisio et al., 2015; Bisio, Avanzino, Biggio, Ruggeri, & Bove, 2017). A particularly interesting form of external feedback is sonification, an online auditory augmentation strategy whereby a sound characteristic, e.g. volume, is associated with, and modulated by silent movement parameters that would not be associated with a sound *per se*, such as action-related kinematics or kinetics (Dubus & Bresin, 2013; Sigrist, Rauter, Riener, & Wolf, 2013). The augmented information can be used to modulate performers' behaviour. For example, the pitch of a sound can be associated with elbow flexion and extension, such that flexion would decrease the pitch and extension would increase it. A video of a tutor executing an action could then be shown, providing not only visual (Holmes & Calmels, 2008), but also sonification-related auditory guidance to the observer. To date, limited research on the topic suggests that sonification of action observation (sAO) yields more accurate perceptual judgments, as well as increased brain activity in sensorimotor areas. Schmitz et al. (2013) instructed participants to observe a breaststroke performed by an avatar, where the relative distance between the wrists and the ankles modulated two different sounds profiles. The sounds were modulated either congruently, or incongruently with the action. Congruent sonification yielded significant more accurate judgment of movement speed, and this was associated to increased functional connectivity between superior temporal sulcus, basal ganglia and the thalamus, which are areas involved in motor control (Park, Coddington, & Dudman, 2020). More recently, Mezzarobba et al. (2018) provided evidence for the effectiveness of sAO of daily activities as an addition to traditional rehabilitation regimes in Parkinson's patients. Three months of sAO induced significant reduction in freezing of gait in people, an improvement that was retained up to a month after the completion of the rehabilitation regime. Taken together, these studies suggest that the audiomotor associations during sAO may augment sensorimotor processing, affording better sensorimotor internal models (Kilner et al., 2007b; Kilner, Friston, & Frith, 2007a).

While AO and MI alone are effective, their combination may improve the effectiveness of interventions using simulated actions. A recent theoretical framework, the dual action simulation hypothesis, suggests that AO and MI can be simultaneously represented in the brain (Eaves, Riach, Holmes, & Wright, 2016). Specifically, it is thought that AO and MI can be represented as two different sensorimotor streams which, according to their contents, can share or compete for computational resources during simulation of actions. Recent studies provide support for this hypothesis (Bruton, Holmes, Eaves, Franklin, & Wright, 2020). Engaging in congruent AOMI, in which a person is asked to imagine the kinaesthetic feeling of same observed action, from the same perspective, induces greater neural activity over sensorimotor areas compared to AO or MI alone (Berends, Wolkorte, Ijzerman, & Van Putten, 2013; Macuga & Frey, 2012; Nedelko, Hassa, Hamzei, Schoenfeld, & Dettmers, 2012; Taube et al., 2015). This increased activity is also reflected in higher motor evoked potentials (MEPs) during AOMI (Bruton et al., 2020; Meers, Nuttall, & Vogt, 2020; Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009; Wright, Williams, & Holmes, 2014; Wright, Wood, Eaves, et al., 2018). AOMI was shown to be effective in rehabilitation of different neurological conditions, such as stroke (Sun, Wei, Luo, Gan, & Hu, 2016) and developmental coordination disorder (Marshall, Wright, Holmes, Williams, & Wood, 2020; Scott, Emerson, Dixon, Tayler, & Eaves, 2019). Within the framework of the dual simulation hypothesis, sonification, once successfully associated to an action, could be integrated into the internal representation of a person, as a bottom-up sensorimotor stream, alongside visual phenomena. This could enhance

sensorimotor interaction, thereby enhancing corticospinal excitability and plasticity (Eaves et al., 2016). In a previous study, we sought to investigate whether sonification could influence combined use of action observation and motor Imagery (sAOMI) of very simple actions (Castro et al., 2021). Sonification of a pinching task did not influence corticospinal excitability, compared to non-sonified conditions and, after the practice, audiomotor plasticity was not influenced by sonification. In this study, we aimed at further exploring sAOMI of a more complex audiomotor association. In addition, we also tested whether practice was able to induce audiomotor association, by assessing post-practice AO and AOMI with and without sonification sound.

2. Methods

2.1. Participants

Twenty-five self-reported neurologically healthy, right-handed young adults were recruited for this study (Table 1). Participants were randomly assigned to either the experimental group (SON, 12 participants), which completed the practice block with sonification, or the control group (CON, 13 participants), who did not receive auditory augmentation during the practice. Prior to the beginning of the experiment, participants completed the Edinburgh Handedness Inventory (Oldfield, 1971) to assess their degree of right-handedness, and were asked to complete a safety screening questionnaire, to assess potential contraindication for the use of Transcranial Magnetic Stimulation (TMS; Rossi, Hallett, Rossini, & Pascual-Leone, 2009, 2011). To assess baseline MI ability, participants completed the third version of the motor imagery questionnaire (MIQ-3; Williams et al., 2012), measuring MI vividness. At the end of the study, each participant received a £20 Amazon gift card.

2.2. Experimental design

Fig. 1a depicts a schematic representation of the experimental procedure. In a single session, we tested corticospinal excitability before and after a practice block, based on congruent and combined AOMI, MI and physical execution of the same action. Assessment of corticospinal excitability, before and after the intervention, was carried out by measuring motor-evoked potentials (MEPs) while participants were at rest, while observing the practiced action (AO), or while they performed congruent kinaesthetic imagery of the action as they observed it (AOMI). Pre-practice tests were completed without auditory augmentation. After the practice block, participants completed the same tests, but engaged in AO and AOMI tests twice, without and with auditory augmentation, respectively. We tested this to assess whether SON group developed an audiomotor resonance following the sonification training. The audiomotor condition was always completed after the silent condition, as there is evidence that even a short audiomotor pairing can establish an association (Launay, Dean, & Bailes, 2016; Ticini, Schutz-Bosbach, Weiss, Casile, & Waszak, 2011). In all tests, participants had a similar posture depicted in the video, composed of holding of a foam a ball with their right hand (Fig. 2a). Congruency between participants' posture and observed action was needed as there is evidence that this type of

Table 1
Demographic data, by group

	SON		CON	
	Mean	SEM	Mean	SEM
Age (years)	26.22	3.08	24.44	2.10
EHI Score	8.89	0.76	9.67	0.33
Internal visual imagery	5.28	0.47	5.75	0.33
External Visual Imagery	5.67	0.28	5.98	0.28
Kinesthetic Imagery	5.33	0.44	5.58	0.33
rMT	41.11	2.18	37.33	1.26

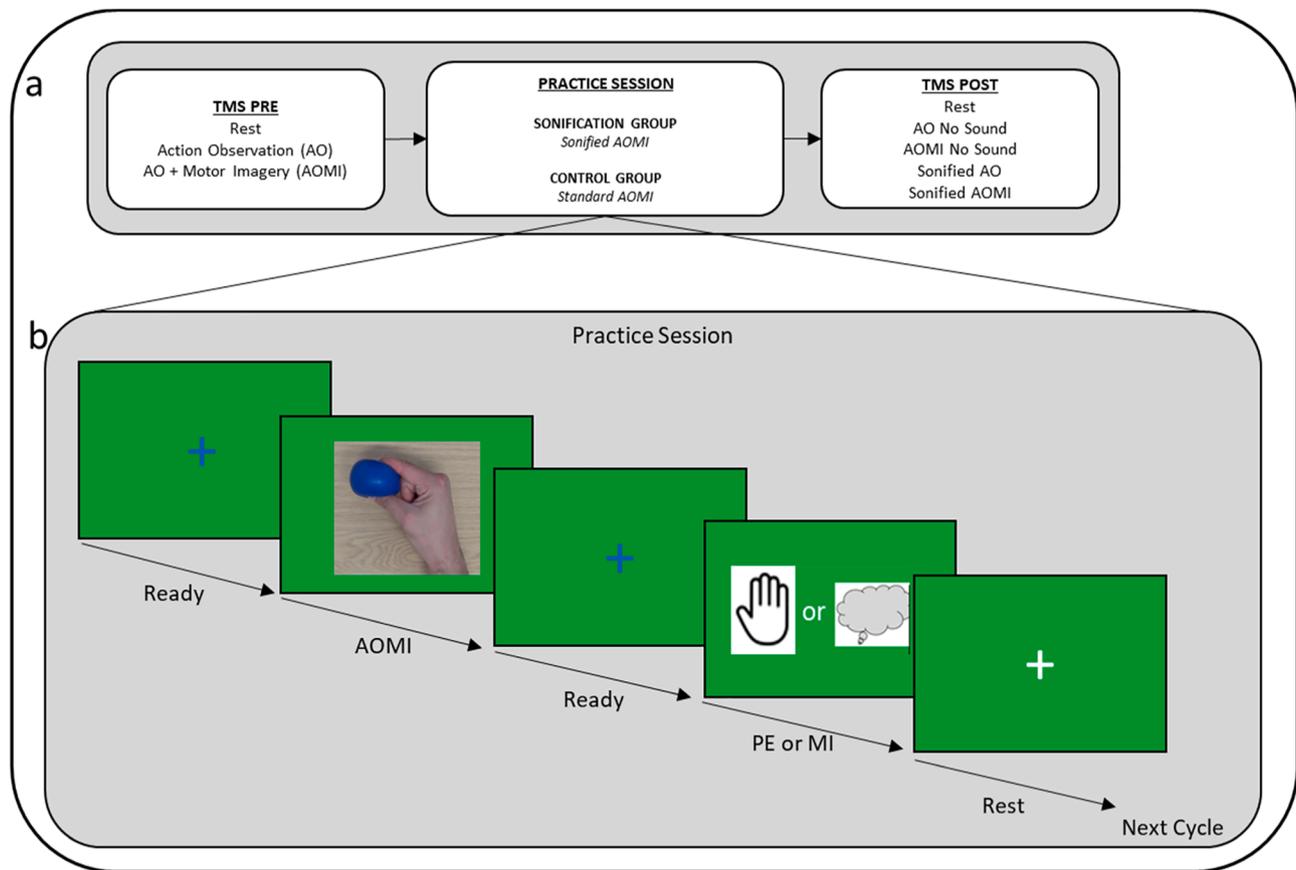


Fig. 1. a. Schematic representation of the experimental design. In a single session, corticospinal excitability measures were collected before and after a practice block, at rest and during AO and AOMI. After the practice, motor-evoked potentials (MEPs) were collected twice during AO and AOMI, without and with sound. b. Schematic representation of stimuli presentation during the practice block. At the beginning of the cycle, participant observed a blue cross (“get ready” cue). After one second, the video of an actor’s hand squeezing a foam ball appeared. Participants were instructed to pay attention to the video, while at the same time imagining themselves performing the action. SON group also received auditory augmentation during AO. After the video, another blue cross appeared, after which participants were asked to either imagine the action they just saw (MI; bubble icon), or physically execute the same action (PE; hand icon). Participants were asked to press a button with their left hand when they completed the simulated or executed action, thus triggering a rest period (white cross) for 5 s.

congruence affects motor resonance during AO (Zimmermann, Toni, & de Lange, 2013), as well as during MI (Saimpont, Malouin, Tousignant, & Jackson, 2012; Vargas et al., 2004).

2.3. Combined action observation and motor imagery practice

The practice block consisted of combined and congruent AOMI, followed by MI and physical execution of the same action. It comprised 48 trials, for an average duration of 30 min. Trials were divided into three blocks one minute of rest between blocks. Fig. 1b depicts the practice structure and stimuli presentation. Participants first observed, while concurrently imagining the kinaesthetic feelings associated with the action they observed, from a first-person perspective (kinaesthetic imagery). In this phase, the SON group listened to the sonification sound too, and they were asked to pay attention to information that this sound may have provided with respect to the action. After the AOMI phase, a blue cross appeared, cuing participants to prepare for the next phase, in which they either imagine the same action (bubble icon appeared on the screen) or physically imitated the same action (hand icon). Executed trials represented 25% of the total trials and were fully randomised. At the end of either MI or PE, participants had to press a button with their left hand to rest for 5 s.

2.4. Task and sonification process

Participants observed and imagined an action in which an actor

squeezed a foam ball with their index and thumb finger, viewed from a first-person perspective. We chose this action because one of the prime effectors for this action, the index finger, was the focus of our stimulated muscle, the FDI. This allowed us to be confident in the dynamics of corticospinal excitability during TMS stimulation. In addition, similar actions have also been used in previous TMS studies (Riach, Holmes, Franklin, & Wright, 2018; van Polanen, Rens, & Davare, 2020). The action lasted about 3 s. The sonification process was performed using a frame-to-frame strategy. Raw videos were recorded at 25 frame per seconds using a Sony HDR-TD3, at a resolution of 1920 × 1080. Sonification was performed using the open-source *Audacity* software, by synthesising a pitch of the same duration of the action. Raw videos and synthesised sound were then exported in the free video editing software *Hitfilm express 2017* (FXHOME Limited, UK), where sound and video were manually synchronised. Sonification consisted of increasing or decreasing the volume of the tone according to the force visibly applied to the ball: as the ball was compressed, the volume of the tone increased, and diminished as the force decreased and the ball expanded back to its original shape. We chose this audiomotor association because it is among the most commonly used mapping in sonification research (Dubus & Bresin, 2013). We chose a synthesised sound because we were also interested in the effects of sonification on audiomotor resonance. We deemed unlikely that such a tone would be able to induce audiomotor resonance per se. However, after audiomotor practice, these type of sounds can induce activity in the motor system, after an audiomotor association has been established. (Launay et al., 2016; Ticini et al., 2011;

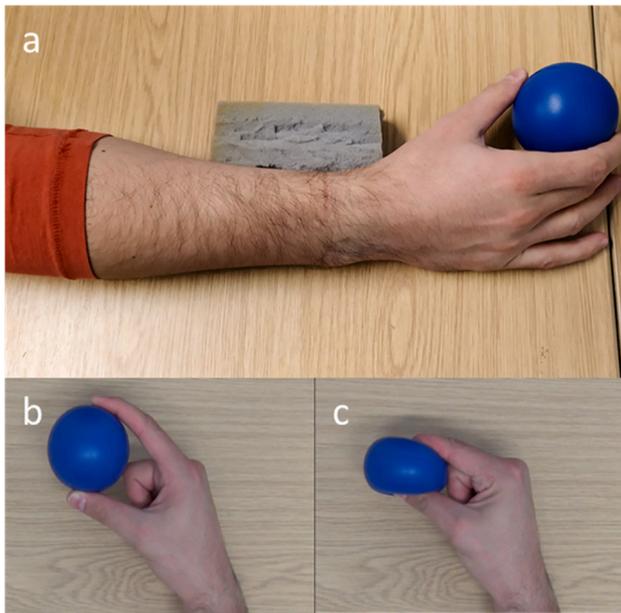


Fig. 2. a. Arm configuration during TMS testing and practice block. Participants were instructed to keep their hands on a table and hold a ball, which rested on the table, in their hands, and participants were asked to relax as much as possible and avoid muscle contractions. To further improve their comfort, a foam mat was placed under their forearm. b. The initial video frame; c. The point in the video at which TMS pulses were delivered (maximal compression).

Ticini, Schütz-Bosbach, & Waszak, 2017).

2.5. Assessment of corticospinal excitability

Assessment of corticospinal excitability was done by collecting MEPs from the right first dorsal interosseous (FDI) muscle. For each condition, twenty-five MEPs were collected, with a stimulation intensity of 130% of the individually defined resting motor threshold (rMT). We chose this stimulation intensity based on previous neurophysiological studies on AO (Aglioti, Cesari, Romani, & Urgesi, 2008; Alaerts, Heremans, Swinnen, & Wenderoth, 2009; Alaerts, Swinnen, & Wenderoth, 2010, 2009; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005; Urgesi, Candidi, Fabbro, Romani, & Aglioti, 2006). However, we acknowledge that a stimulation intensity of 110% of rMT has been recommended (Loporto, Mcallister, Williams, Hardwick, & Holmes, 2011), as it is less likely to evoke direct waves (Di Lazzaro et al., 2004, 2012). Participants sat on a chair in front of a 24" LCD monitor, at a viewing distance of one meter from the screen. In rest condition, TMS pulses were delivered while participants directed their visual attention at a fixation cross, at the centre of the screen, and engaged in a secondary, non-motoric task, consisting of a countdown from 200 to 0 (Kumpulainen et al., 2014). During AO and AOMI tests participants kept an arm configuration congruent with the action (Fig. 2a), and TMS pulses were delivered when the video depicted the maximal squeezing phase (Fig. 2c). TMS monophasic pulses were delivered using a Magstim 200 (Magstim Company, Whitland, U.K.), using a 70 mm figure-of-eight stimulation coil, oriented to induce posterior-to-anterior current. Muscle responses were collected using Ag/AgCl electrodes arranged in a bipolar, belly-tendon setup. Participants' skin area was shaved (if needed), abraded using an abrasive paste and cleaned using isopropyl alcohol swabs. After preparation, and before any test, the hotspot for TMS stimulation was determined as coil position that evoked MEPs of the largest amplitude, at the same intensity, and then marked on participants' scalp with a soft-tip pen. rMT was estimated, using adaptive threshold hunting technique (Ah Sen et al., 2017; Awiszus, 2011), which allowed us to determine rMT with a reduced number of TMS stimulations, thereby improving

participants' comfort. At the end of the experiment, we collected the maximum evoked muscle twitch (M_{max}) evoked by peripheral magnetic stimulation at the FDI muscle. This was done by placing the TMS coil on participants' right elbow, between the olecranon and the medial epicondyle, with the coil handle perpendicular to the direction of the ulnar nerve, to induce current flow in the nerve with the monophasic stimulator (Lampropoulou, Nowicky, & Marston, 2012). To determine M_{max} , we collected five evoked responses for responses ranging between 20% and 70% of the maximum stimulus output, in incremental steps of 10%. Surface electromyography (EMG) and evoked responses were recorded using Signal (v.6, CED, UK) and amplified at a gain of 1000 and sampled at 4 kHz. To reduce the influence of external artefacts, an online band-pass filter (5–2000 Hz) was applied. TMS pulses were delivered through synchronized stimulus presentation, using TTL output triggers generated by E-Prime software (v 3.0; Psychology Software Tools, Pittsburgh, PA), and sent to the magnetic stimulator.

2.6. Data and statistical analysis

2.6.1. MEPs analysis

Peak-to-peak MEP amplitude and background EMG were calculated for every trial using a custom-made script in Signal software (CED, v6.05; UK). For background EMG, we calculated the root mean square of muscle activity during 100 ms prior to the TMS pulse. Given participants' hand posture during TMS stimulation, trials where background EMG was greater than 300 μ V were excluded from the analysis. MEPs were normalised and expressed as percentage of M_{max} , using the following formula:

$$\text{Normalised MEP} = 100 \times \frac{\text{MEP}}{M_{max}} \quad (1)$$

We chose this normalization method according to the rationale that M_{max} measures the maximum possible contraction, and it is thought to be stable against transient changes in excitability (Palmieri, Ingersoll, & Hoffman, 2004). In addition, this normalization method is commonly used to express spinal excitability (Palmieri et al., 2004). Unless otherwise specified, in later sections MEPs will refer to normalized, not raw, values.

2.6.2. Post-Training audiomotor resonance

To assess audiomotor resonance arising from the sonification practice, we calculated the percentage change between pre- and post-practice raw MEP values. For both AO and AOMI, we compared pre- with post-practice completed with or without sonification sound.

$$\text{MEP No Sound} = 100 \times \frac{\text{Pre} - \text{Post no Sound}}{\text{Pre}} \quad (2)$$

$$\text{MEP Sound} = 100 \times \frac{\text{Pre} - \text{Post Sound}}{\text{Pre}} \quad (3)$$

Both CON and SON completed this. Since CON was not exposed to the sound during the training, we did not expect modulation of corticospinal excitability with sound, so it was used as control for SON.

2.6.3. Statistical analysis

Statistical comparisons were carried out using SPSS. Outliers were assessed using z-scores; values greater than ± 2.99 were considered as outliers and removed from the analysis. Data distribution was assessed with the Shapiro-Wilk test. Handedness, MIQ and corticospinal excitability changes between AO/AOMI and rest were analysed using nonparametric tests. For the analysis of corticospinal excitability changes between pre- and post-practice at rest and during AO and AOMI, we ran a mixed ANOVA with factors TIME (2 levels, pre and post) and GROUP (2 levels, SON and CON). For the analysis of audiomotor resonance during AO and AOMI, we ran a mixed ANOVA with factors SOUND (2 levels, sound and no sound) and GROUP (SON and CON).

3. Results

Table 1 provide a summary of participants' demographic data, by group. There were no significant between-group differences in handedness ($z = -0.748, p = 0.454$), rMT ($z = 0.906, p = 0.365$), Internal visual imagery ($z = -0.164, p = 0.870$), external visual imagery ($z = -0.301, p = 0.764$) and kinaesthetic imagery ($z = -0.164, p = 0.870$). There were no significant differences in bgEMG levels between AO and rest ($z = -1.789, p = 0.074$). Engaging in AO did not result in a significant modulation of corticospinal excitability, compared to resting conditions ($z = 1.655, p = 0.098$). On the other hand, engaging in AOMI resulted in a significant increase in corticospinal excitability, compared to rest ($z = 2.44, p = 0.015$). However, bgEMG analysis revealed significantly differences in muscle activity between AOMI and rest ($z = -2.731, p = 0.006$).

3.1. Effects of practice on corticospinal excitability at rest and during AO and AOMI

Practice effect was assessed by comparing MEPs amplitude before and after the practice, at rest, as well as during AO and AOMI (Table 2). There were no significant differences in bgEMG levels in all three conditions (p greater than 0.05; see S1 for statistical details). At rest, (Fig. 3a), there was a significant increase of MEPs amplitude after the practice: main effect of TIME, $F(1, 23) = 15.03; p = 0.001, N^2_p = 0.395$. No TIME \times GROUP interaction was detected: $F(1, 23) = 0.289; p = 0.596, N^2_p = 0.012$. During AO (Fig. 3b), there was a significant increase in MEP amplitude after the practice: main effect of TIME, $F(1,23) = 27.450; p < 0.001; N^2_p = 0.544$. There was a trend towards significance for the interaction TIME \times GROUP: $F(1,23) = 3.509; p = 0.074; N^2_p = 0.132$. Lastly, during AOMI (Fig. 3c) there was a significant increase of MEP amplitude after the practice: main effect of TIME on MEP amplitude: $F(1,23) = 7.742; p = 0.011; N^2_p = 0.252$. No TIME \times GROUP interactions were found: $F(1,23) = 0.311; p = 0.582; N^2_p = 0.13$.

3.2. Effects of sonification on audiomotor resonance after practice

After the practice block, we collected MEPs during AO and AOMI with and without sonification sound. MEPs with sound were always collected last. We compared these with Pre-practice measures, to explore whether sonification induced an audiomotor association (Table 3). During AO (Fig. 4a), a rmANOVA revealed no statistical differences for SOUND, $F(1,22) = 1.834, p = 0.189, N^2_p = 0.077$, and no SOUND \times GROUP interactions were found: $F(1,22) = 0.014, p = 0.906$

Table 2

Descriptive Statistics for corticospinal excitability measures. MEPs are expressed as percentage of M_{max} .

		Mean	Median	SD	SEM	95% CI	
						Lower	Upper
Control	Rest						
	Pre	17.01	12.94	10.41	3.00	10.40	23.63
	Post	25.29	20.73	13.33	3.85	16.81	33.76
AO	Pre	18.55	15.22	10.77	3.11	11.71	25.39
	Post	27.47	25.46	14.46	4.17	18.28	36.65
	Sound	24.45	21.93	14.58	4.21	15.18	33.71
AOMI	Pre	21.89	18.71	13.46	3.88	13.34	30.44
	Post	29.73	28.50	12.02	3.47	22.09	37.36
	Sound	28.60	26.16	14.90	4.30	19.13	38.07
Sonification	Rest						
	Pre	17.38	13.92	12.48	3.76	9.00	25.77
	Post	21.83	18.82	13.61	4.10	12.69	30.97
AO	Pre	17.69	17.88	12.00	3.62	9.63	25.75
	Post	21.97	15.59	15.26	4.60	11.72	32.22
	Sound	20.14	17.26	12.67	3.82	11.62	28.65
AOMI	Pre	20.49	20.17	11.64	3.51	12.67	28.31
	Post	24.73	23.75	12.97	3.91	16.02	33.45
	Sound	23.68	22.42	14.35	4.33	14.04	33.33

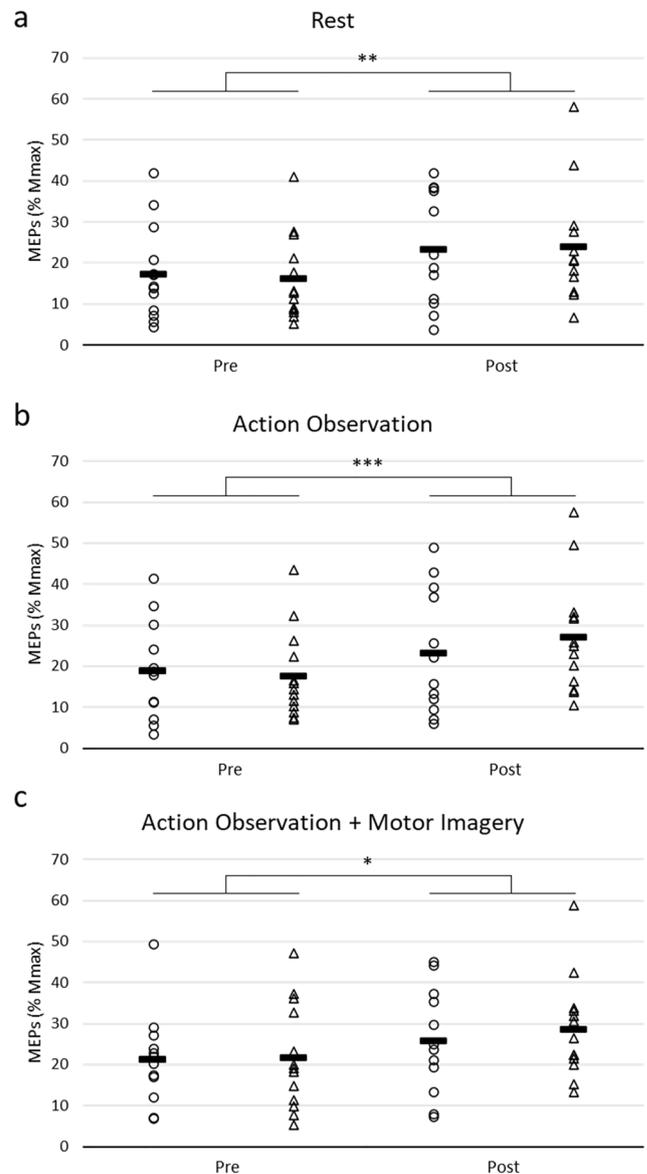


Fig. 3. Corticospinal excitability measures before and after the practice block, measured at rest (a), during Action Observation (b), and during combined action observation and motor imagery (c). Circle represents SON group (12 participants), while the triangles represent CON groups (13 participants). Black bars represent group-level means. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

Table 3

Descriptive statistics for percentage change in MEP values pre- and post-practice, measured without and with sonification sound.

		Mean	Median	SD	SEM	95% CI	
						Lower	Upper
Control	AO						
	Sound	46.04	42.40	66.10	19.93	1.63	90.44
	No Sound	60.62	53.10	37.81	11.40	35.22	86.02
AOMI	Sound	44.07	44.72	52.44	15.81	8.85	79.30
	No Sound	48.63	37.35	66.67	20.10	3.83	93.42
Sonification	AO						
	Sound	22.13	2.46	50.99	14.72	-10.26	54.53
	No Sound	32.48	19.59	55.87	16.13	-3.02	67.97
AOMI	Sound	13.22	8.67	39.34	11.36	-11.77	38.21
	No Sound	22.63	8.42	45.69	13.19	-6.40	51.66

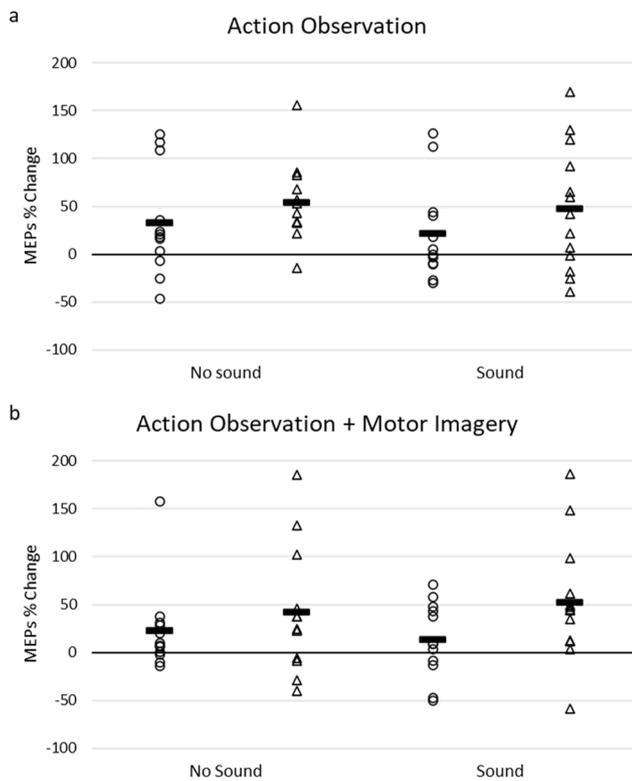


Fig. 4. Pre-post percentage change comparisons on the influence of auditory stimulation while engaging in AO (a) and AOMI (b). After the practice block, we measured corticospinal excitability during AO and AOMI in two conditions, with and without sonification sound. The 'No Sound' condition represents comparisons between pre and post-no sound, while the 'Sound' condition represents comparisons between and post-sound. For both AO and AOMI, no significance differences were found between the SON group (12 participants; circles) and CON group (13 participants; triangles). Black bars represent group-level means.

$N^2_p = 0.001$. Similarly, during AOMI (Fig. 4b) there were no significant main effect of SOUND, $F(1,22) = 0.385$, $p = 0.541$, $N^2_p = 0.017$. No SOUND \times GROUP interaction emerged: $F(1,22) = 0.281$, $p = 0.601$, $N^2_p = 0.013$.

4. Discussion

The aim of this study was to investigate the effects of sAOMI on corticospinal excitability and the associated development of audiomotor association. Participants completed a practice block composed of AOMI, motor imagery and execution of the same action. SON group received auditory augmentation during AOMI, while CON group did not receive any extrinsic auditory stimulation.

4.1. Effects of sAOMI on corticospinal excitability

At the end of the practice block, participants' corticospinal excitability was significantly higher than pre-training measures at rest, as well as during AO and AOMI. However, we did not find significant differences between the two groups. The fact that corticospinal excitability after the practice block increased in both groups is in line with literature suggesting that, among others, practice induces changes in corticospinal excitability, due to an unmasking of silent cortico-cortical connections (Dayan & Cohen, 2011; Rosenkranz, Kacar, & Rothwell, 2007; Ziemann, Ilić, Pauli, Meintzschel, & Ruge, 2004), resulting in long-term potentiation of circuits involved in practice. This neural mechanism is also involved in observational and mental practice (Avanzino et al., 2015; Lepage et al., 2012).

With regard to sonification, our results are in line with our previous study on sAOMI (Castro et al., 2021), but seem to be in contrast with existing literature on sAO, which suggest that observing an action with congruent sonification induces a more precise perceptual judgment about movement speed in healthy population, associated with an increased activation in areas involved in sensorimotor transformations and motor control (Schmitz et al., 2013). In addition, sAO was associated with significant improvement of a variety of measures of freezing of gait in parkinsonians (Mezzarobba et al., 2018). Lastly, research on movement sonification generally reports that congruent sonification has beneficial effects in inducing changes in performance (Schaffert, Janzen, Mattes, & Thaut, 2019; Sigrist et al., 2013). Some differences between our study and others may explain this disparity. In our study we used sonified congruent AOMI to deliver auditory augmentation. Compared to AO or MI alone, AOMI induces increased neural activity, as measured with fMRI (Macuga & Frey, 2012), and EEG (Eaves, Behmer, & Vogt, 2016), which is ultimately reflected in increased corticospinal excitability, compared to AO and MI alone (Bruton et al., 2020; Meers et al., 2020; Sakamoto et al., 2009; Wright et al., 2014; Wright, Wood, Eaves, et al., 2018). It is possible that the inclusion of MI during sAO could have masked the effect of sonification, as recent studies show that MI seems to have a major effect on corticospinal excitability during AOMI (Bruton et al., 2020; Meers et al., 2020). However, MI implies a functional equivalence in internally-induced predictions of sensorimotor characteristics of an action (Kilteni et al., 2018; Kilteni, Engeler, Boberg, & Maurex, 2021), including a sense of agency (Nierula, Spanlang, Martini, Sanchez-vives, Nikulin, Taylor, & Farina, 2020). Thus, it could be hypothesised that sonification during AOMI would result in a better matching between top-down and bottom-up processing. It is possible that sonification did not exert its effects because the ball-squeezing action chosen for this study was not challenging enough for our participants. This is akin to many common daily tasks, which people without movement disorders can perform with little effort. We chose this task because research show that MI vividness – the clarity of the generated image – affects corticospinal excitability, thus suggesting that even though a task is easy to perform, it may not be easy to imagine (Lebon, Byblow, Collet, Guillot, & Stinear, 2012; Williams, Pearce, Loporto, Morris, & Holmes, 2012). However, MIQ results suggests that, on average, our participants were 'good imagers' (Marchesotti, Bassolino, Serino, Bleuler, & Blanke, 2016; Vuckovic & Osuagwu, 2013). Thus, it is possible that this action was simple to internally simulate, and sonification did not exert its augmenting influence.

Another explanation for the lack of effect of sonification may be an increase in cognitive effort during the practice. Despite research on sonification generally reports a reduction in cognitive load (Dyer, Stapleton, & Rodger, 2015), a study by Ronsse et al. (2011) suggests that compared to visual augmentation, sonification may induce slower rate of learning at the beginning of a coordinative bimanual task practice, associated with increased attentional demands, evidenced by increased activity in the dorsolateral prefrontal cortex, a brain area widely involved in attentional processing (Gottlieb, 2012; Suzuki & Gottlieb, 2013). It is possible that auditory processing may have interfered with AOMI processing during the practice block. Different studies suggests that, within the right condition, AO requires relatively low cognitive effort, especially when compared to MI (Nota, Chartrand, Levkov, Montefusco-Siegmund, & DeSouza, 2017). However, neural activity during AO is modulated by different factors, such as background with the observed action seems to influence motor resonance (Riach et al., 2018), visual attention (D'Innocenzo, Gonzalez, Nowicky, Williams, & Bishop, 2017; Gandevia & Rothwell, 1987; Wright, Wood, Franklin, et al., 2018) and cognitive effort (Puglisi, Leonetti, Cerri, & Borroni, 2018). Recent studies also suggest that changing the relation between the content of the imagined and observed action seems to influence MEP amplitude and attentional measures. To explore this, studies usually contrast three forms of AOMI: congruent, coordinative, and conflicting. In the first one, the observed and imagined action has the same content,

while in coordinative AOMI it may be the same but from a different perspective, or a complementary action which may assist the other. On the other hand, in conflicting AOMI the observed and imagined actions are different and not compatible with each other. Recently, Bruton et al. (2020) reported that corticospinal excitability was lower in conflicting AOMI, compared to congruent AOMI. Interestingly, engaging in coordinative and conflicting AOMI also increased attentional demands and cognitive efforts, compared to congruent AOMI. The fact that engaging in different forms of AOMI is associated with different neurocognitive signatures is in line with a representationalist framework originally developed by Cisek and Kalaska (2010), but later adapted to action simulation by Eaves et al. (2016), suggesting that the brain represents different potential actions and, through a process of competition resolution, it interfaces with the environment, selecting the most appropriate one, given prior intentions, predictions and sensations sampled (c. f. Bestmann & Duque, 2016; Derosiere & Duque, 2020 for an account of action preparation and competition resolution). If the action was very simple to imagine for the participants, and the sonification did not exert its augmenting effects, it may have acted as a distractor, interfering with sensorimotor processing in a similar fashion as coordinative and incongruent AOMI. Future studies, with a larger sample size, are needed to further explore and add robustness to the relationship between the value of an augmented sensory information and action simulation. In this study, we focussed on congruent AOMI, but it is possible that sonification may have beneficial effects on other forms of AOMI. Especially with coordinative AOMI, sonification could be associated to a complementary aspect of an observed action, while a person engages in MI. To the best of our knowledge this question remains unanswered.

4.2. Effects of sonification of audiomotor association

After the practice block, we tested corticospinal excitability during AO and AOMI without or with sonification sound. Both groups did not show significant differences in corticospinal excitability between the two conditions. For CON, no corticospinal excitability change was expected, as sonification sound was novel to them. On the other hand, SON practiced with sAOMI, so the development of an audiomotor association could be hypothesised. Action sounds interact with the sensorimotor system, similarly to AO, by mapping the sound into the listener's own sensorimotor system, through a process of multisensory convergence (Aglioti & Pazzaglia, 2011). Even though action and non-action sounds are thought to be processed differently (Pineda et al., 2013), it is possible to associate a non-action sound to a motor response. Music is a chief example for this: Listening to the sound of a practised piece activates brain areas responsible for physical execution of the same action (Baumann et al., 2007; Lahav, Saltzman, & Schlaug, 2007). In addition, it has been reported that it is possible to associate a sound with a simple button press. Ticini et al. (2011) trained participants to press two buttons, one with the index and the other with the little finger, which were associated to two different tones. After the training, playing the sounds evoked increased MEPs in the fingers used to press the button during the association practice. Interestingly, if the relationship between muscle and button was reversed, the pattern of corticospinal excitability was reversed too, such that it preserved the audiomotor relationship developed during the practice. This suggests that the association is not just tone-muscle, but of higher order, associating the sound to the goal of the action. More recently, Ticini et al. (2017) reported that when the association was established, a training of equal time inducing opposite association was not enough to dissociate the audiomotor resonance developed during the training.

In this study, we used a synthesised sound, and the audiomotor association – volume of a sound associated with perceived kinetics – is a common audiomotor mapping in sonification research (Dubus & Bresin, 2013). However, our results are in line with a possible distracting role of sonification for sensorimotor computations underlying action simulation. Sensory information are thought to be processed in early sensory

cortices, which deal with the physical nature of the stimulus, and then integrated by higher order multisensory areas (Rizzolatti & Sinigaglia, 2010), where they are integrated into the representation of the body and the outside environment, which are thought to be used to make top-down predictions about perception and actions (Friston et al., 2011; Kilner et al., 2007a). Research on processing of auditory distractors during movement suggest a role of parietal areas in the resolution of the conflict provided by the distractor (Bigliassi, Karageorghis, Nowicky, Wright, & Orgs, 2018), which allows performance to be carried out without detriment. In this study, if sonification did not exert its augmenting effect, possibly because the task was too simple, it is possible that the sound was not fully integrated the visual stimuli and predictions about the sensory consequences of the imagined action. In other words, it is possible that processing of auditory information was attenuated, to prevent performance detriment. Interestingly, Franklin, Wright, and Holmes (2020) reported that if a sound of a congruent action-related word was provided during AO, corticospinal excitability was significantly higher than AO alone, as well as if the word was not action-related and incongruent with the observed action. Taken together, this may be suggestive of a critical role of the epistemic value of a sensory information during sensorimotor processing underlying AO and AOMI. Our discussion on the relationship between sonification sound and action simulation remains, however, somewhat speculative, and future studies are needed to further explore this area. Specifically, our study used a relatively easy tasks to perform, and a more complex task may induce different results. In addition, a larger sample size would add robustness to the analysis.

5. Conclusions

The purpose of this study was to explore whether sonification of combined action observation and motor imagery (sAOMI) influenced corticospinal excitability, and whether a practice block based on sAOMI, MI and physical execution of the same action influenced the establishment of an audiomotor association. Our results suggest that, at least for simpler tasks, sonification does not influence corticospinal excitability and, on the contrary it may act as a distractor, preventing an audiomotor association from being developed. Future studies are needed to further explore the relationship between auditory augmentation and action simulation, to establish the optimal audiomotor mapping to maximise neural activity and practice-dependent plasticity.

Funding

This study was funded by Brunel University London Ph.D Studentship.

CRedit authorship contribution statement

Fabio Castro: Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **Paulina Anna Bryjka:** . **Giovanni Di Pino:** Writing - review & editing. **Aleksandra Vuckovic:** Writing - review & editing. **Alexander Nowicky:** Software, Writing - review & editing. **Daniel Bishop:** Supervision, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandc.2021.105768>.

References

- Abbruzzese, G., Avanzino, L., Marchese, R., & Pelosin, E. (2015). Action observation and motor imagery: innovative cognitive tools in the rehabilitation of Parkinson's disease, 2015. DOI: 10.1155/2015/124214.
- Aglioti, S. M., Cesari, P., Romani, M., & Urgesi, C. (2008). Action anticipation and motor resonance in elite basketball players. *Nature Neuroscience*, 11(9), 1109–1116. <https://doi.org/10.1038/nn.2182>.
- Aglioti, S. M., & Pazzaglia, M. (2011). Sounds and scents in (social) action. *Trends in Cognitive Sciences*, 15(2), 47–55. <https://doi.org/10.1016/j.tics.2010.12.003>.
- Ah Sen, C. B., Fassett, H. J., El-Sayes, J., Turco, C. V., Hameer, M. M., & Nelson, A. J. (2017). Active and resting motor threshold are efficiently obtained with adaptive threshold hunting. *PLoS ONE*, 12(10), 1–9. <https://doi.org/10.1371/journal.pone.0186007>.
- Alaerts, K., Heremans, E., Swinnen, S. P., & Wenderoth, N. (2009). How are observed actions mapped to the observer's motor system? Influence of posture and perspective. *Neuropsychologia*, 47(2), 415–422. <https://doi.org/10.1016/j.neuropsychologia.2008.09.012>.
- 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(10), 1148–1155. <https://doi.org/10.1016/j.cortex.2008.10.005>.
- Alaerts, K., Swinnen, S. P., & Wenderoth, N. (2010). Observing how others lift light or heavy objects: Which visual cues mediate the encoding of muscular force in the primary motor cortex? *Neuropsychologia*, 48(7), 2082–2090. <https://doi.org/10.1016/j.neuropsychologia.2010.03.029>.
- Avanzino, L., Gueugneau, N., Bisio, A., Ruggeri, P., Papaxanthis, C., & Bove, M. (2015). Motor cortical plasticity induced by motor learning through mental practice. *Frontiers in Behavioral Neuroscience*, 9(April), 105. <https://doi.org/10.3389/fnbeh.2015.00105>.
- Awiszus, F. (2011). Fast estimation of transcranial magnetic stimulation motor threshold: Is it safe? *Brain Stimulation*, 4(1), 50–57. <https://doi.org/10.1016/j.brs.2010.06.002>.
- Bassolino, M., Campanella, M., Bove, M., Pozzo, T., & Fadiga, L. (2014). Training the motor cortex by observing the actions of others during immobilization. *Cerebral Cortex*, 24(12), 3268–3276. <https://doi.org/10.1093/cercor/bht190>.
- Baumann, S., Koenke, S., Schmidt, C. F., Meyer, M., Lutz, K., & Jancke, L. (2007). A network for audio-motor coordination in skilled pianists and non-musicians. *Brain Research*, 1161(1), 65–78. <https://doi.org/10.1016/j.brainres.2007.05.045>.
- Berends, H. I., Wolkorte, R., Ijzerman, M. J., & Van Putten, M. J. A. M. (2013). Differential cortical activation during observation and observation-and-imagination. *Experimental Brain Research*, 229(3), 337–345. <https://doi.org/10.1007/s00221-013-3571-8>.
- Bestmann, S., & Duque, J. (2016). Transcranial magnetic stimulation: Decomposing the processes underlying action preparation. *Neuroscientist*, 22(4), 392–405. <https://doi.org/10.1177/1073858415592594>.
- Bigliassi, M., Karageorghis, C. I., Nowicky, A. V., Wright, M. J., & Orgs, G. (2018). Effects of auditory distraction on voluntary movements: Exploring the underlying mechanisms associated with parallel processing. *Psychological Research*, 82(4), 720–733. <https://doi.org/10.1007/s00426-017-0859-5>.
- Bisio, A., Avanzino, L., Biggio, M., Ruggeri, P., & Bove, M. (2017). Motor training and the combination of action observation and peripheral nerve stimulation reciprocally interfere with the plastic changes induced in primary motor cortex excitability. *Neuroscience*, 348, 33–40. <https://doi.org/10.1016/j.neuroscience.2017.02.018>.
- Bisio, A., Avanzino, L., Gueugneau, N., Pozzo, T., Ruggeri, P., & Bove, M. (2015). Observing and perceiving: A combined approach to induce plasticity in human motor cortex. *Clinical Neurophysiology*, 126(6), 1212–1220. <https://doi.org/10.1016/j.clinph.2014.08.024>.
- Bرتون, A. M., Holmes, P. S., Eaves, D. L., Franklin, Z. C., & Wright, D. J. (2020). Neurophysiological markers discriminate different forms of motor imagery during action observation. *Cortex*, 124, 119–136. <https://doi.org/10.1016/j.cortex.2019.10.016>.
- Buccino, G. (2014). Action observation treatment: A novel tool in neurorehabilitation. *Philosophical Transactions of the Royal Society B*, 369, 20130185. <https://doi.org/10.1098/rstb.2013.0185>.
- Castro, F., Osman, L., Di Pino, G., Vuckovic, A., Nowicky, A., & Bishop, D. (2021). Does sonification of action simulation training impact corticospinal excitability and audiomotor plasticity? *Experimental Brain Research*, In Press. <https://doi.org/10.1007/s00221-021-06069-w>.
- Cisek, P., & Kalaska, J. F. (2010). Neural mechanisms for interacting with a world full of action choices. *Annual Review of Neuroscience*, 33, 269–298. <https://doi.org/10.1146/annurev-neuro.051508.135409>.
- D'Innocenzo, G., Gonzalez, C. C., Nowicky, A. V., Williams, A. M., & Bishop, D. T. (2017). Motor resonance during action observation is gaze-contingent: A TMS study. *Neuropsychologia*, 103(November 2016), 77–86. <https://doi.org/10.1016/j.neuropsychologia.2017.07.017>.
- Dayan, E., & Cohen, L. G. (2011). Neuroplasticity subserving motor skill learning. *Neuron*, 72(3), 443–454. <https://doi.org/10.1016/j.neuron.2011.10.008>.
- Derosiere, G., & Duque, J. (2020). Tuning the corticospinal system: How distributed brain circuits shape human actions. *Neuroscientist*. <https://doi.org/10.1177/1073858419896751>.
- Di Lazzaro, V., Oliviero, A., Pilato, F., Saturno, E., Dileone, M., Mazzone, P., ... Rothwell, J. (2004). The physiological basis of transcranial motor cortex stimulation in conscious humans. *Clinical Neurophysiology*, 115(2), 255–266. <https://doi.org/10.1016/j.clinph.2003.10.009>.
- Di Lazzaro, V., Profice, P., Ranieri, F., Capone, F., Dileone, M., Oliviero, A., & Pilato, F. (2012). I-wave origin and modulation. *Brain Stimulation*, 5(4), 512–525. <https://doi.org/10.1016/j.brs.2011.07.008>.
- Dubus, G., & Bresin, R. (2013). A systematic review of mapping strategies for the sonification of physical quantities. *PLoS ONE*, 8(12). <https://doi.org/10.1371/journal.pone.0082491>.
- Dyer, J. F., Stapleton, P., & Rodger, M. W. M. (2015). Sonification as concurrent augmented feedback for motor skill learning and the importance of mapping design. *The Open Psychology Journal*, 8(1), 192–202. <https://doi.org/10.2174/1874350110508010192>.
- Eaves, D. L., Behmer, L. P., & Vogt, S. (2016). EEG and behavioural correlates of different forms of motor imagery during action observation in rhythmical actions. *Brain and Cognition*, 106, 90–103. <https://doi.org/10.1016/j.bandc.2016.04.013>.
- Eaves, D. L., Riach, M., Holmes, P. S., & Wright, D. J. (2016). Motor imagery during action observation: A brief review of evidence, theory and future research opportunities. *Frontiers in Neuroscience*, 10(NOV). <https://doi.org/10.3389/fnins.2016.00514>.
- Franklin, Z. C., Wright, D. J., & Holmes, P. S. (2020). Using action-congruent language facilitates the motor response during action observation: A combined transcranial magnetic stimulation and eye-tracking study. *Journal of Cognitive Neuroscience*, 32(4), 634–645. https://doi.org/10.1162/jocn_a.01510.
- Friston, K., Mattout, J., & Kilner, J. (2011). Action understanding and active inference. *Biological Cybernetics*, 104(1–2), 137–160. <https://doi.org/10.1007/s00422-011-0424-z>.
- Gandevia, S. C., & Rothwell, J. C. (1987). Knowledge of motor commands and the recruitment of human motoneurons. *Brain*, 110(5), 1117–1130. <https://doi.org/10.1093/brain/110.5.1117>.
- Gottlieb, J. (2012). Attention, Learning, and the Value of Information. *Neuron*, 76(2), 281–295. <https://doi.org/10.1016/j.neuron.2012.09.034>.
- Guillot, A., Di Rienzo, F., MacIntyre, T., Moran, A., & Collet, C. (2012). Imagining is not doing but involves specific motor commands: A review of experimental data related to motor inhibition. *Frontiers in Human Neuroscience*, 6(September), 1–22. <https://doi.org/10.3389/fnhum.2012.00247>.
- Holmes, P., & Calmels, C. (2008). A neuroscientific review of imagery and observation use in sport. *Journal of Motor Behavior*, 40(5), 433–445. <https://doi.org/10.3200/JMBR.40.5.433-445>.
- Ingram, T. G. J., Kraeutner, S. N., Solomon, J. P., Westwood, D. A., & Boe, S. G. (2016). Skill acquisition via motor imagery relies on both motor and perceptual learning. *Behavioral Neuroscience*, 130(2), 1–9. <https://doi.org/10.1037/bne0000126>.
- Jeanerod, M. (2001). Neural simulation of action: A unifying mechanism for motor cognition. *NeuroImage*, 14(1), S103–S109. <https://doi.org/10.1006/nimg.2001.0832>.
- Jeanerod, M. (2004). Actions from within. *International Journal of Sport and Exercise Psychology*, 2(4), 376–402. <https://doi.org/10.1080/1612197x.2004.9671752>.
- Kilner, J. M. (2011). More than one pathway to action understanding. *Trends in Cognitive Sciences*. <https://doi.org/10.1016/j.tics.2011.06.005>.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007a). The mirror-neuron system: A Bayesian perspective. *Neuroreport*, 18(16), 619–623.
- Kilner, J. M., Friston, K. J., & Frith, C. D. (2007b). Predictive coding: An account of the mirror neuron system. *Cognitive Processing*. <https://doi.org/10.1007/s10339-007-0170-2>.
- Kilteni, K., Andersson, B. J., Houborg, C., & Ehrsson, H. H. (2018). Motor imagery involves predicting the sensory consequences of the imagined movement. *Nature Communications*, 9(1). <https://doi.org/10.1038/s41467-018-03989-0>.
- Kilteni, K., Engeler, P., Boberg, I., & Maurex, L. (2021). No evidence for somatosensory attenuation during action observation of self-touch.
- Kraeutner, S. N., MacKenzie, L. A., Westwood, D. A., & Boe, S. G. (2015). Characterizing skill acquisition through motor imagery with no prior physical practice. *Journal of Experimental Psychology: Human Perception and Performance*, 42(2), 257–265. <https://doi.org/10.1037/xhp0000148>.
- Kumpulainen, S., Avela, J., Gruber, M., Bergmann, J., Voigt, M., Linnamo, V., & Mrachacz-Kersting, N. (2014). Differential modulation of motor cortex plasticity in skill- and endurance-trained athletes. *European Journal of Applied Physiology*, 115(5), 1107–1115. <https://doi.org/10.1007/s00421-014-3092-6>.
- Lahav, A., Saltzman, E., & Schlaug, G. (2007). Action representation of sound: Audiomotor recognition network while listening to newly acquired actions. *Journal of Neuroscience*, 27(2), 308–314. <https://doi.org/10.1523/JNEUROSCI.4822-06.2007>.
- Lampropoulou, S. I., Nowicky, A. V., & Marston, L. (2012). Magnetic versus electrical stimulation in the interpolation twitch technique of elbow flexors. *Journal of Sports Science and Medicine*, 11(4), 709–718.
- Launay, J., Dean, R. T., & Bailes, F. (2016). Rapid learning of associations between sound and action through observed movement. A TMS study. *Psychomusicology*, 26(1), 35–42. <https://doi.org/10.1037/pmu0000131>.
- Lebon, F., Byblow, W. D., Collet, C., Guillot, A., & Stinear, C. M. (2012). The modulation of motor cortex excitability during motor imagery depends on imagery quality. *European Journal of Neuroscience*, 35(2), 323–331. <https://doi.org/10.1111/j.1460-9568.2011.07938.x>.
- Lepage, J.-F., Morin-Moncet, O., Beaulieu, V., de Beaumont, L., Champoux, F., & Theoret, H. (2012). Occlusion of LTP-like plasticity in human primary motor cortex by action observation. *Plos One*, 7(6), 3–8. <https://doi.org/10.1371/journal.pone.0038754>.
- Loporto, M., McAllister, C., Williams, J., Hardwick, R., & Holmes, P. (2011). Investigating central mechanisms underlying the effects of action observation and imagery through transcranial magnetic stimulation. *Journal of Motor Behavior*, 43(5), 361–373. <https://doi.org/10.1080/00222895.2011.604655>.
- Macuga, K. L., & Frey, S. H. (2012). Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized.

- NeuroImage*, 59(3), 2798–2807. <https://doi.org/10.1016/j.neuroimage.2011.09.083>.
- Marchesotti, S., Bassolino, M., Serino, A., Bleuler, H., & Blanke, O. (2016). Quantifying the role of motor imagery in brain-machine interfaces. *Scientific Reports*, 6(1), 24076. <https://doi.org/10.1038/srep24076>.
- Marshall, B., Wright, D. J., Holmes, P. S., Williams, J., & Wood, G. (2020). Combined action observation and motor imagery facilitates visuomotor adaptation in children with developmental coordination disorder. *Research in Developmental Disabilities*, 98 (August 2019), 103570. <https://doi.org/10.1016/j.ridd.2019.103570>.
- Meers, R., Nuttall, H. E., & Vogt, S. (2020). Motor imagery alone drives corticospinal excitability during concurrent action observation and motor imagery. *Cortex*, 126, 322–333. <https://doi.org/10.1016/j.cortex.2020.01.012>.
- Mezzarobba, S., Grassi, M., Pellegrini, L., Catalan, M., Kruger, B., Furlanis, G., ... Bernardis, P. (2018). Action observation plus sonification. A novel therapeutic protocol for Parkinson's patient with freezing of gait. *Frontiers in Neurology*, 8(JAN), 1–13. <https://doi.org/10.3389/fneur.2017.00723>.
- Mulder, Th. (2007). Motor imagery and action observation: Cognitive tools for rehabilitation. *Journal of Neural Transmission*, 114(10), 1265–1278. <https://doi.org/10.1007/s00702-007-0763-z>.
- Mulder, Theo, Zijlstra, S., Zijlstra, W., & Hochstenbach, J. (2004). The role of motor imagery in learning a totally novel movement. *Experimental Brain Research*, 154(2), 211–217. <https://doi.org/10.1007/s00221-003-1647-6>.
- Nedelko, V., Hassa, T., Hamzei, F., Schoenfeld, M. A., & Dettmers, C. (2012). Action imagery combined with action observation activates more corticomotor regions than action observation alone. *Journal of Neurologic Physical Therapy*, 36(4), 182–188. <https://doi.org/10.1097/NPT.0b013e318272cad1>.
- Nierula, B., Spanlang, B., Martini, M., Sanchez-vives, M. V., Nikulin, V. V., Taylor, J., & Farina, D. (2020). Agency and responsibility over virtual movements controlled through different paradigms of brain – computer interface, 0, 1–16. doi: 10.1113/JP278167.
- Nota, P. M., Chartrand, J. M., Levkov, G. R., Montefusco-Siegmund, R., & DeSouza, J. F. X. (2017). Experience-dependent modulation of alpha and beta during action observation and motor imagery. *BMC Neuroscience*, 18(1), 1–14. <https://doi.org/10.1186/s12868-017-0349-0>.
- Oldfield, R. (1971). The assessment and the analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, 9, 97–113.
- Ostry, D. J., & Gribble, P. L. (2016). Sensory plasticity in human motor learning. *Trends in Neurosciences*, 39(2), 114–123. <https://doi.org/10.1016/j.tins.2015.12.006>.
- Ostry, D. M., Mattar, A. A. G., Wong, J., & Gribble, P. L. (2010). Somatosensory plasticity and motor learning. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 30(15), 5384–5393. <https://doi.org/10.1523/JNEUROSCI.4571-09.2010>.
- Palmieri, R. M., Ingersoll, C. D., & Hoffman, M. A. (2004). The Hoffmann reflex: Methodologic considerations and applications for use in sports medicine and athletic training research. *Journal of Athletic Training*, 39(3), 268–277.
- Park, J., Coddington, L. T., & Dudman, J. T. (2020). Basal Ganglia circuits for action specification. *Annual Review of Neuroscience*, 43(September), 485–507. <https://doi.org/10.1146/annurev-neuro-070918-050452>.
- Pascual-Leone, A., Nguyen, K. T., Cohen, A. D., Brasil-Neto, J. P., Cammarota, A., & Hallett, M. (1995). Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *Journal of Neurophysiology*, 74(3), 1037–1045.
- Pineda, J. A., Grichanik, M., Williams, V., Trieu, M., Chang, H., & Keyser, C. (2013). EEG sensorimotor correlates of translating sounds into actions. *Frontiers in Neuroscience*, 7 (7 DEC), 1–9. <https://doi.org/10.3389/fnins.2013.00203>.
- Puglisi, G., Leonetti, A., Cerri, G., & Borroni, P. (2018). Attention and cognitive load modulate motor resonance during action observation. *Brain and Cognition*, 128 (October), 7–16. DOI: S0278262618301131.
- Riach, M., Holmes, P. S., Franklin, Z. C., & Wright, D. J. (2018). Observation of an action with a congruent contextual background facilitates corticospinal excitability: A combined TMS and eye-tracking experiment. *Neuropsychologia*, 119(July), 157–164. <https://doi.org/10.1016/j.neuropsychologia.2018.08.002>.
- Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27(1), 169–192. <https://doi.org/10.1146/annurev.neuro.27.070203.144230>.
- Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience*. <https://doi.org/10.1038/nrn2805>.
- Romani, M., Cesari, P., Urgesi, C., Facchini, S., & Aglioti, S. M. (2005). Motor facilitation of the human cortico-spinal system during observation of bio-mechanically impossible movements. *NeuroImage*, 26(3), 755–763. <https://doi.org/10.1016/j.neuroimage.2005.02.027>.
- Ronsse, R., Puttemans, V., Coxon, J., Goble, D., Wagemans, J., Wenderoth, N., & Swinnen, S. (2011). Motor learning with augmented feedback: Modality-dependent behavioral and neural consequences. *Cerebral Cortex*, 21(6), 1283–1294. <https://doi.org/10.1093/cercor/bhq209>.
- Rosenkranz, K., Kacar, A., & Rothwell, J. (2007). Differential modulation of motor cortical plasticity and excitability in early and late phases of human motor learning. *The Journal of Neuroscience*, 27(44), 12058–12066. <https://doi.org/10.1523/JNEUROSCI.2663-07.2007>.
- Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2009). Safety, ethical considerations, and application guidelines for the use of transcranial magnetic stimulation in clinical practice and research. *Clinical Neurophysiology*, 120(12), 2008–2039. <https://doi.org/10.1016/j.clinph.2009.08.016>.
- Rossi, S., Hallett, M., Rossini, P. M., & Pascual-Leone, A. (2011). Screening questionnaire before TMS: An update. *Clinical Neurophysiology*, 122(8), 1686. <https://doi.org/10.1016/j.clinph.2010.12.037>.
- Rozand, V., Lebon, F., Papaxanthis, C., & Lepers, R. (2014). Does a mental training session induce neuromuscular fatigue? *Medicine and Science in Sports and Exercise*, 46 (10), 1981–1989. <https://doi.org/10.1249/MSS.0000000000000327>.
- Saimpont, A., Malouin, F., Touseignant, B., & Jackson, P. L. (2012). The influence of body configuration on motor imagery of walking in younger and older adults. *Neuroscience*, 222, 49–57. <https://doi.org/10.1016/j.neuroscience.2012.06.066>.
- Sakamoto, M., Muraoka, T., Mizuguchi, N., & Kanosue, K. (2009). Combining observation and imagery of an action enhances human corticospinal excitability. *Neuroscience Research*, 65(1), 23–27. <https://doi.org/10.1016/j.neures.2009.05.003>.
- Schaffert, N., Janzen, T. B., Mattes, K., & Thaut, M. H. (2019). A review on the relationship between sound and movement in sports and rehabilitation. *Frontiers in Psychology*, 10(February), 244. <https://doi.org/10.3389/fpsyg.2019.00244>.
- Schmitz, G., Mohammadi, B., Hammer, A., Heldmann, M., Samii, A., Münte, T. F., & Effenberg, A. O. (2013). Observation of sonified movements engages a basal ganglia frontocortical network. *BMC Neuroscience*, 14(1), 32. <https://doi.org/10.1186/1471-2202-14-32>.
- Scott, M. W., Emerson, J. R., Dixon, J., Tayler, M. A., & Eaves, D. L. (2019). Motor imagery during action observation enhances automatic imitation in children with and without developmental coordination disorder. *Journal of Experimental Child Psychology*, 183, 242–260. <https://doi.org/10.1016/j.jecp.2019.03.001>.
- Sigrist, R., Rauter, G., Riener, R., & Wolf, P. (2013). Augmented visual, auditory, haptic, and multimodal feedback in motor learning: A review. *Psychonomic Bulletin & Review*, 20(1), 21–53. <https://doi.org/10.3758/s13423-012-0333-8>.
- Sun, Y., Wei, W., Luo, Z., Gan, H., & Hu, X. (2016). Improving motor imagery practice with synchronous action observation in stroke patients. *Topics in Stroke Rehabilitation*, 23(4), 245–253. <https://doi.org/10.1080/10749357.2016.1141472>.
- Suzuki, M., & Gottlieb, J. (2013). Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. *Nature Neuroscience*, 16(1), 98–104. <https://doi.org/10.1038/nn.3282>.
- Taube, W., Mouthon, M., Leukel, C., Hoogewoud, H. M., Annoni, J. M., & Keller, M. (2015). Brain activity during observation and motor imagery of different balance tasks: An fMRI study. *Cortex*, 64, 102–114. <https://doi.org/10.1016/j.cortex.2014.09.022>.
- Ticini, L. F., Schütz-Bosbach, S., & Waszak, F. (2017). Mirror and (absence of) counter-mirror responses to action sounds measured with TMS. *Social Cognitive and Affective Neuroscience*, 12(11), 1748–1757. <https://doi.org/10.1093/scan/nsx106>.
- Ticini, L., Schütz-Bosbach, S., Weiss, C., Casile, A., & Waszak, F. (2011). When sounds become action: Higher-order representation of newly learned action sounds in the human motor system. *Journal of Cognitive Neuroscience*, 24(2), 464–474. <https://doi.org/10.1162/jocn.2010.02002>.
- Urgesi, C., Candidi, M., Fabbro, F., Romani, M., & Aglioti, S. M. (2006). Motor facilitation during action observation: Topographic mapping of the target muscle and influence of the onlooker's posture. *European Journal of Neuroscience*, 23(9), 2522–2530. <https://doi.org/10.1111/j.1460-9568.2006.04772.x>.
- van Polanen, V., Rens, G., & Davare, M. (2020). The role of the anterior intraparietal sulcus and the lateral occipital cortex in fingertip force scaling and weight perception during object lifting. *Journal of Neurophysiology*, 124(2), 557–573. <https://doi.org/10.1152/JN.00771.2019>.
- Vargas, C. D., Olivier, E., Craighero, L., Fadiga, L., Duhamel, J. R., & Sirigu, A. (2004). The influence of hand posture on corticospinal excitability during motor imagery: A transcranial magnetic stimulation study. *Cerebral Cortex*, 14(11), 1200–1206. <https://doi.org/10.1093/cercor/bhh080>.
- Vogt, S., Di Rienzo, F., Collet, C., Collins, A., & Guillot, A. (2013). Multiple roles of motor imagery during action observation. *Frontiers in Human Neuroscience*, 7(November), 1–13. <https://doi.org/10.3389/fnhum.2013.00807>.
- Vuckovic, A., & Osuagwu, B. A. (2013). Using a motor imagery questionnaire to estimate the performance of a Brain-Computer Interface based on object oriented motor imagery. *Clinical Neurophysiology*, 124(8), 1586–1595. <https://doi.org/10.1016/j.clinph.2013.02.016>.
- Williams, J., Pearce, A. J., Loporto, M., Morris, T., & Holmes, P. S. (2012). The relationship between corticospinal excitability during motor imagery and motor imagery ability. *Behavioural Brain Research*, 226(2), 369–375. <https://doi.org/10.1016/j.bbr.2011.09.014>.
- Williams, S. E., Cumming, J., Ntoumanis, N., Nordin-Bates, S. M., Ramsey, R., & Hall, C. (2012). Further validation and development of the movement imagery questionnaire. *Journal of Sport & Exercise Psychology*, 34, 621–646. <https://doi.org/10.1123/jsep.34.5.621>.
- Wright, D. J., Williams, J., & Holmes, P. S. (2014). Combined action observation and imagery facilitates corticospinal excitability. *Frontiers in Human Neuroscience*, 8 (NOV), 1–9. <https://doi.org/10.3389/fnhum.2014.00951>.
- Wright, D. J., Wood, G., Eaves, D. L., Bruton, A. M., Frank, C., & Franklin, Z. C. (2018). Corticospinal excitability is facilitated by combined action observation and motor imagery of a basketball free throw. *Psychology of Sport and Exercise*, 39(February), 114–121. <https://doi.org/10.1016/j.psychsport.2018.08.006>.
- Wright, D. J., Wood, G., Franklin, Z. C., Marshall, B., Riach, M., & Holmes, P. S. (2018). Directing visual attention during action observation modulates corticospinal

- excitability. *PLoS ONE*, 13(1), 1–15. <https://doi.org/10.1371/journal.pone.0190165>.
- Ziemann, U., Ilić, T. V., Pauli, C., Meintzschel, F., & Ruge, D. (2004). Learning modifies subsequent induction of long-term potentiation-like and long-term depression-like plasticity in human motor cortex. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 24(7), 1666–1672. <https://doi.org/10.1523/JNEUROSCI.5016-03.2004>.
- Zimmermann, M., Toni, I., & de Lange, F. P. (2013). Body posture modulates action perception. *Journal of Neuroscience*, 33(14), 5930–5938. <https://doi.org/10.1523/JNEUROSCI.5570-12.2013>.