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The effect of expertise on kinesthetic motor imagery of complex actions

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Abstract

The ability to mentally simulate an action by recalling the body sensations relative to the real execution is referred to as kinesthetic motor imagery (MI). Frontal and parietal motor-related brain regions are generally engaged during MI. The present study aimed to investigate the time course and neural correlates of complex action imagery and possible effects of expertise on the underlying action representation processes. Professional ballet dancers and controls were presented with effortful and effortless ballet steps and instructed to mentally reproduce each movement during EEG recording. Time-locked MI was associated with an Anterior Negativity (AN) component (400-550 ms) that was larger in dancers relative to controls. The AN was differentially modulated by the motor content (effort) as a function of ballet expertise. It was more negative in response to effortful (than effortless) movements in control participants only. This effect also had a frontal distribution in controls and a centro-parietal distribution in dancers, as shown by the topographic maps of the scalp voltage. The source reconstruction (swLORETA) of the recorded potentials in the AN time-window showed enhanced engagement of prefrontal regions in controls (BA 10/47) relative to dancers, and occipitotemporal (BA 20) and bilateral sensorimotor areas in dancers (BA6/40) compared with controls. This evidence seems to suggest that kinesthetic MI of complex action relied on visuomotor simulation processes in participants with acquired dance expertise. Simultaneously, increased cognitive demands occurred in participants lacking in motor knowledge with the specific action. Hence, professional dance training may lead to refined action representation processes.

Text

1. Introduction

Motor imagery (MI) has been defined as a dynamic state in which an action is mentally simulated in the absence of any real movement execution (Decety, 1996). As part of the motor representation phenomenon (Jeannerod, 1994; 2001), it is considered a conscious process and implies feelings similar to those produced by actual action performance. Growing attention has been given to this complex and heterogeneous mental ability (Hanakawa, 2016) to investigate action representation and support sports practice (Ridderinkhof & Brass, 2015) and physical rehabilitation therapy (Dickstein & Deutsch, 2007).

A common distinction exists between kinesthetic (KMI) and visual (VMI) motor imagery processes (Annett, 1995). While KMI involves a focus on simulating the sensorimotor and bodily/proprioceptive sensations that occur during action execution, VMI implies the imagination of the scene from a first-person (internal) or third-person (external) perspective (Jiang et al., 2015). Functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) evidence have shown distinct but partially overlapping neural substrates underlying these two MI types (Guillot et al., 2009; 2014; Kilintary et al., 2016; Ptak et al., 2017). The engagement of the supplementary motor area (SMA, anterior and posterior part), inferior parietal lobule (IPL, lateral and anterior part), frontal areas (BA 9, 24, 44), basal ganglia (putamen and nucleus caudatus), and cerebellum has been observed during KMI of finger movements (Guillot et al., 2009). VMI of the same action sequences engaged the occipital visual (BA 17, 18, 19) and superior parietal (BA 5, 7) regions, together with SMA (posterior and superior part) and posterior IPL. Therefore, while visual areas are largely involved in VMI, motor-related regions are specifically engaged during KMI (Mizuguchi et al., 2017).

Increased imaginative ability (Guillot et al., 2008) and the subsequent perceived vividness of the mental image (Lorey et al., 2011) have also been associated with increased activity in the premotor cortex (PM), IPL, superior parietal lobule (SPL), and putamen. Consistent with the simulation hypothesis suggested by Jeannerod (1994, 2001), this evidence suggests functional similarities between the cognitive processes underlying MI and motor preparation for actual action execution (Kilteny et al., 2018; Ruffino et al., 2017). Further support comes from studies involving mental chronometry and rotation of body stimuli, with the former showing a correspondence between actual and mental duration of action (Munzert, 2008; Reed, 2002), and the latter revealing the engagement of the precentral sulcus (Zacks, 2008). Finally, while the role of parietal areas (i.e., left anterior parietal cortex) is quite

consistent between MI investigations (Oosterhof et al., 2012), the involvement of the primary motor cortex (M1) is still debated (Munzert et al., 2009). TMS (Loporto et al., 2011) and EEG (Neuper & Pfurtscheller, 2010) studies seem to confirm the M1 recruitment, in contrast to two recent meta-analyses (imaging studies) reporting activity only during action execution (Hardwick et al., 2017; Héту et al., 2013). For instance, lateralized readiness potentials (LRP, linked to motor preparation; Leuthold & Jentzsch, 2002) of similar latency and waveform have been reported during MI and execution of simple hand and foot movements. The comparable polarity inversion depending on the body part used suggested a somatotopic organization of M1 response (Carrillo-de-la-Peña et al., 2006; Ehrsson et al., 2003).

The present EEG study investigated the time course and neural correlates of KMI of complex action (i.e., whole-body technical dance gesture) by comparing the brain activity of participants of different levels of motor knowledge with the action itself. Professional ballet dancers and non-dancer controls were presented with videos depicting technical ballet gestures and instructed to reproduce each movement mentally. Two categories of gestures were created based on the degree of muscular effort required by actual action execution: effortful vs. effortless movements (i.e., three turns on the spot vs. one turn).

The modulation of effort information contained within movement has been previously used as a tool to investigate action representation during MI. The imagination of repetitive effortful (vs. less tiring) actions (i.e., running, lifting heavy objects) leads to enhanced breath and heart rate (Decety et al., 1991; 1993; Paccalin et al., 2000), together with increased arterial pressure (i.e., trunk or leg movements against gravity; Demougeot et al., 2009). Thus, general anticipatory central mechanisms are thought to prepare the organism for the forthcoming effortful motor task, through the increased activity of the autonomic nervous system. MI of effortful action is also associated with increased corticospinal excitability (MEPs amplitude), as reported in TMS studies involving MI of finger (Helm et al., 2015), wrist (Tatemoto et al., 2017), and foot (Kato & Kanosue, 2017) movements.

A ballet dance repertoire includes several technical movements that require different degrees of muscular effort despite being kinematically similar, for example, in the use of the space (i.e., jumps and turns on the spot). Moreover, a dance expertise framework has been previously used in action observation and imagination studies (Cross et al., 2006; di Nota et al., 2017), along with frameworks of sport (Filgueiras et al., 2017; Milton et al., 2008; Wei & Luo, 2010) and musical practice (Lotze et al., 2013). Professional training is associated with a more efficient neural network for specialized motor planning and visuomotor integration (Chang et

al., 2011; Milton et al., 2007). For instance, reduced brain volume activity has been found during MI of pre-shot routine (preparation for the golf swing) in expert golf players (vs. controls; Milton et al., 2007), together with greater engagement of the SPL, lateral PM (dorsal) and occipital regions. Activity in the limbic regions (i.e., posterior cingulate cortex, amygdala-forebrain complex, and basal ganglia) has been reported in aforementioned controls likely indicating difficulty in filtering irrelevant information due to lack of motor representation. In addition, a more refined and organized neural network during MI of archery shooting (i.e., engagement of the SMA, especially in the left hemisphere) has been shown in expert archers when compared with controls (Chang et al., 2011), that in turn, required a broader recruitment of brain regions (i.e., PM, SMA, M1, inferior parietal and frontal cortex, basal ganglia, and cerebellum). In the present study, only the dancers were expected to incorporate effort-related information (encoded at a visuomotor level) during the recollection of the motor program of the imagined ballet steps.

Moreover, high-density EEG was here used to combine the well-known temporal resolution of event-related potentials (ERPs) with the relatively good spatial resolution provided by swLORETA source reconstruction (Cebolla et al., 2017; Palmero-Soler et al., 2007). Previous EEG studies compared the brain activity during imagined and real execution of hand and foot actions, revealing event-related desynchronization (ERD) in alpha/mu (i.e., 8-12 Hz; Pfurtscheller et al., 1997; 2001; Neuper et al., 2005) and beta (i.e., 13-30 Hz; Formaggio et al., 2010; McFarland et al., 2000) frequency bands over contralateral sensorimotor regions (i.e., SMA). MI modulation (Olsson & Nyberg, 2010) as a function of movement complexity (Kuhtz-Buschbeck et al., 2003; Yi et al., 2013) and body parts involved (Szameitat et al., 2007; Yuan et al., 2010) has also been proposed. Of particular importance is the study by Cebolla and colleagues (2015), in which MI of repetitive and more complex movements (tennis ball throwing vs. rest) led to a negative fronto-central ERPs maximum peaking at 300 ms and 1000 ms. In the time-frequency domain, contralateral mu (9-13 Hz) ERD (530-750 ms) was reported during MI, followed by fronto-central theta (3-5 Hz) event-related synchronization (ERS; 750-900 ms), and fronto-parieto-occipital high alpha/low beta ERD (1000-1150 ms). The authors interpreted these results, respectively, as an index of sensorimotor activity, attention allocation, and motor planning and proprioceptive/visual information processing.

Based on existing literature, it was expected to find a negative response over anterior sites (Anterior Negativity, AN) as an electrophysiological marker of kinematic MI processing of complex action (Cebolla et al., 2015; Weber et al., 2016). It was hypothesized to observe

modulations of the AN amplitude contingent on both ballet expertise (Fourkas et al., 2008; Orlandi et al., 2017; 2019) and motor content (Helm et al., 2015; Kato et al., 2017). If KMI requires the engagement of visuomotor processes, ballet dancers should be able to recall sensorimotor representations due to their extensive training (larger AN). They were also expected to encode effort information during movement observation (Orlandi et al., 2020), consistent with previous evidence on professional musicians (vs. controls; Pau et al, 2013). In contrast, MI of effortful (vs. effortless) movements would result in enhanced cognitive demands (larger AN) in controls lacking in specific motor expertise with ballet, due to increased effort-related kinematic information (Proverbio et al., 2009). Finally, in support of these hypotheses, two source reconstructions (swLORETA) were performed to investigate the neural generators of the effort-related AN. It was expected to find the enhanced engagement of sensorimotor and occipitotemporal regions in dancers (Milton et al., 2007), and prefrontal areas in controls (Wei & Lou, 2010).

2. Materials and Methods

2.1 Participants

Thirty-two female volunteers took part in this study. Sixteen were professional ballet dancers (mean age 25.94 years, SD = 5.26) with an average of 20 years of dance experience (SD = 5.73) and a mean age of acquisition (onset of training) of 5 years (SD = 1.98). They all received formal training in ballet (mean = 9.06 years, SD = 5.73), and were professional dancers, choreographers, and/or teachers (demographic information is reported in Table 1). The other 16 volunteers were female control university students (mean age 25 years, SD = 2.83) with no experience whatsoever with dance, gymnastics, or martial arts. To avoid a confound of opposite- vs. own-sex effects (during body perception), participants were all females, right-handed, and heterosexual. The Italian version of the Edinburgh Handedness Inventory was employed to assess right-handedness. All the participants had normal or corrected-to-normal vision and reported no history of neurological illness or drug abuse. The experiment received the approval of the ethical committee of the University of Milano – Bicocca, and was conducted with the understanding and the written consent of each volunteer.

2.2 Stimuli creation

Six professional male ballet dancers were recorded while individually performing technical ballet movements belonging to the male and female common repertoire. This included a variety of turns, jumps, and steps. A total of 354 color videos were obtained. Male dancers were selected because greater skeletal muscle mass has been reported in male than female individuals (Janssen et al., 2000). Thus, the effort information conveyed by muscle contraction and action kinematics (Alaerts et al., 2010) was maximized. Specifically, 50% of the steps required a great muscular effort to be executed (177 effortful movements), while the other 50% required less effort (177 effortless movements). For instance, the dancers performed both a series of single turns on the spot (within a 2 seconds window) requiring little muscular effort, and a series of multiple turns (3-4 turns in a 2 seconds window) requiring much more effort. The lists of technical ballet steps are reported in Table 1 as Supplementary Material. A Nikon D7000 Reflex placed on a tripod recorded the videos (frame rate of 25 fps). The original clips depicted the entire movement of each dancer, from the preparation (i.e., in the case of a *pirouette*: preparation with feet in the fifth position) to the final pose (feet in fourth final position). The whole-body was visible and kept at the center of the scene by moving the camera on the horizontal axis. The dancers wore adherent dark clothes to emphasize the musculature of the body and contrast the light grey color of the empty rehearsal space (floor and background). Once recorded, the clips were post-produced using Adobe Premiere Pro CC 2015 (version 9.0). In particular, they were silenced and trimmed to include the climax of the movement (synchronized at 1000 ms; see Fig 1) together with 1000 ms before and after that apex (i.e., the maximum height of a jump). Thus, each video lasted exactly 2000 ms (see Video1 for a few examples of the stimuli). The lighting condition was kept constant during all the days of recording, ensuring the equiluminance of the stimuli ($\cong 1.75$ fL). The final size of the videos was 32 x 23 cm, subtending a visual angle of 15° 18' x 11° 15' when displayed during the experiment.

2.3 Stimuli validation

Twenty female judges took part in a behavioral validation study to assess whether each movement was perceived as effortful or effortless. Ten were professional dancers and ballet teachers (mean age 38.9 years, SD = 11.22) with 26 years of ballet experience (26.2 years, SD = 8.75). The other 10 participants were control volunteers (mean age 39.7 years, SD = 14.97) with no expertise regarding dance, gymnastics, or martial arts. The judges were presented with the 354 stimuli (PowerPoint presentation), displayed on the PC monitor in pseudo-randomized

order. They were instructed to observe each stimulus and verbally rate the degree of muscular effort required to perform the movement. A dichotomic response was allowed (Boolean variable): relatively little effort (indicated as 0) vs. considerable effort (indicated as 1). The selection criterion for the stimuli to be used in the main experiment relied on the concordance rate between professional judges. Specifically, the videos that didn't reach 70% of concordance in the evaluations were discarded. 326 stimuli (163 effortful and 163 effortless) were selected, counterbalanced for kinematics and space parameters, and used in the present investigation.

The rating values of the two groups were also subjected to a repeated measures ANOVA to assess possible expertise-related differences in the effort judgment. ANOVA with one between-groups factor (group: dancers, controls) and one within-groups factor (effort: effortful, effortless) was performed on the individual ratings of perceived effort. Effortful stimuli received higher ratings (0.87, SE = 0.018) compared with effortless stimuli (0.11, SE = 0.019), as shown by the significant main effect of effort factor [$F(1, 18) = 1548.68, p < 0.0001, \eta_p^2 = 0.99$]. Moreover, the significant interaction between group and effort factors [$F(1, 18) = 8.997, p < 0.01, \eta_p^2 = 0.33$] and relevant Duncan's posthoc test showed that the controls (0.83, SE = 0.02) rated the effortful stimuli as less demanding compared with the dancers (0.92, SE = 0.02). The ratings regarding the effortless steps did not differ between groups of judges ($p = 0.49$). Overall, the control judges (relative to dancers) seemed to underestimate (see Fig 2) the effort required to reproduce the effortful steps.

2.4 Task and Procedure

Participants underwent motor imagery training before EEG-cap placement to ensure that all volunteers had a concrete idea and understanding of the meaning of kinematic motor imagery, regardless of dance expertise. They were placed in front of the experimenter who reproduced a series of movements belonging to both daily-life (i.e., touch the floor, jump forward) and ballet (i.e., *plié* with feet in the first position, *échappée*) repertoires. They were instructed to carefully observe each step and perform twice three different tasks (See Fig 3). Firstly, they had to observe the action and physically reproduce it as soon as the experimenter stopped. Secondly, they were instructed to observe the action, reproduce it, and then imagine executing it without any real movement. Thirdly, they had to observe the experimenter and directly imagine reproducing the action, similar to the main task expected during EEG recording. The last task also allowed the participants to become familiarized with the relatively fast timing of the main EEG experiment. Importantly, during the imagination phases, the participants were advised to

recall all the muscular, sensorimotor, and proprioceptive sensations that occurred during the actual execution on the step. A kinesthetic imagery approach was encouraged rather than a mere visualization of the movement, together with the use of a first-person perspective. After the first four movements, the participants were explicitly asked about the vividness of their imaginary performance (i.e., the ability to feel body-related sensations). The training phase ended only once the participant reported a full understanding of the imagery process and felt confident about the recalled execution-related body sensations (indicated as intense or moderately intense).

Once the imagery training (which lasted approximately 10 minutes) was concluded, the EEG-cap was placed on the head of the participants. After that, volunteers were seated in an acoustically and electrically shielded cabin, facing a high-resolution VGA computer screen 114 cm away from their eyes. Stimuli were presented using *Evoke v2.2* (ANT Neuro, Hengelo, The Netherlands). Each trial consisted of a video clip (2000 ms), followed by a red fixation cross on an isoluminant light grey background (inter-stimulus interval, ISI: 900 ms \pm 100 ms), and a subsequent blue fixation cross (3000 ms). The volunteers were instructed to observe each video clip carefully and mentally imagine reproducing the observed action once the red cross changed to blue (see Fig 4). As in the previous training phase, we encouraged a kinesthetic imagery approach from a first-person perspective. Moreover, they were asked to keep their eyes on the fixation cross for the entire duration of a run to minimize eye gaze, blinks, and head movements. Twelve different runs lasting 2.88 minutes were created to include an equal number of effortful and effortless movements. To account for potential familiarization/habituation effects of dancer identity, stimuli were counterbalanced by displaying different dancers every trial. Before EEG recording, the participants were presented with two additional sequences (composed of movement discarded during the validation phase) to become familiar with the experimental task and setting (training phase). All the participants were blinded to the aim of the study and stimuli properties.

2.5 EEG recording and data analysis

EEG was continuously recorded from 128 scalp sites located according to the 10–5 International System (Oostenveld & Praamstra, 2001) at a sampling rate of 512 Hz, using *EEProbe v2.2* (ANT Neuro, Hengelo, The Netherlands). The same software was also used for data analysis. Horizontal and vertical eye movements were also recorded (electrooculogram, EOG) using 4 electrodes (placed on the outer canthus of both eyes, and above the eyebrows)

embedded in the EEG-cap. Averaged mastoids served as the reference lead. The EEG and electrooculogram were amplified and filtered with a half-amplitude band-pass of 0.16–70 Hz and a notch of 50 Hz. Electrode impedance was kept below 5 k Ω . Computerized artifact rejection was performed before averaging to discard epochs in which eye movements, blinks, excessive muscle potentials, or amplifier blocking occurred. The rejection criterion for this automatized procedure was based on peak-to-peak amplitudes exceeding 50 μ V and applied to the entire EEG recordings. EEGs were also manually inspected to avoid undetected artifacts. EEG epochs were synchronized with the colour change of the fixation cross (visual cue for KMI). ERPs were averaged considering –100 ms before the stimulus onset and 1000 ms after the onset. They were subjected to a band-pass filter of 0.16–30 Hz. ERPs were identified and measured with reference to the average baseline voltage computed as the 100 ms before the stimulus onset. The electrode sites and ERPs' latency were chosen based on the maximum amplitude reached by the components of interest (Picton et al., 2000), and in accordance with previous literature (Cebolla et al., 2015; Weber et al., 2016). ERP averages were computed as a function of group (dancers, controls) and stimulus type (effortful vs. effortless). The mean area voltage of the Anterior Negativity (AN) component was measured at Aff1-Aff2, F3-F4, and FFC1h-FFC2h electrode sites during the 400-550 ms time window. The effect size for the statistically significant factors was estimated using partial eta squared (η_p^2), and posthoc comparisons were computed using Duncan's test. Normal distribution of data was assessed by mean of the Kolmogorov-Smirnov test ($p > 0.1$), and Greenhouse-Geisser correction for non-sphericity was applied when appropriate. Overall, the ERP data were subjected to multifactorial repeated measures ANOVA with one between-groups factor (2 levels: dancers, controls) and three within-groups factors, including: effort (2 levels: effortful, effortless), hemisphere (2 levels: left, right), and electrode factors (3 levels: AFF1-2, F3-4, FFC1h-2h).

Standardized and Weighted Low-Resolution Electromagnetic Tomography (swLORETA) was applied to the difference waves obtained by subtracting the ERPs elicited by the effortless stimuli from those evoked by effortful stimuli between 400-550 ms in both groups of participants. LORETA, which is a discrete linear solution to the inverse EEG problem, corresponds to the 3-D distribution of neuronal electric activity that yields maximum similarity (i.e., maximum synchronization), in terms of orientation and strength, between neighboring neuronal populations (represented by adjacent voxels). In this study, an improved version of the sLORETA (*standardized* low-resolution electromagnetic tomography) was used, which incorporates a singular value decomposition-based lead field *weighting* (swLORETA;

Palmero-Soler et al., 2007). The following characteristics for source space were included: 5 mm of grid spacing (the distance between two calculation points) and estimated SNR (Signal-to-Noise Ratio defines the regularization; a higher SNR value leads to less regularization and less blurred results) equal to three. swLORETA was performed on group data to identify statistically significant electromagnetic dipoles ($p < 0.05$), in which as the magnitude increases, the significance of the group differences increases.

3. Results

3.1 Anterior Negativity, AN (400-550 ms)

The ANOVA performed on the amplitude values of the AN component showed a main effect of the group factor [$F(1, 30) = 7.018, p < 0.02, \eta_p^2 = 0.19$]. The negativity was larger in dancers (-2.11 μV , SE = 0.28) than controls (-1.05 μV , SE = 0.28). Fig 5 illustrates the grand average waveforms (ERPs) recorded over all 128 sites of the scalp as a function of the group.

The significant interaction between group and effort factors [$F(1, 30) = 11.703, p < 0.003, \eta_p^2 = 0.28$] and relevant posthoc tests showed that the AN elicited by the effortless movements ($p = 0.002$) was larger in dancers (-2.37 μV , SE = 0.28) than controls (-0.83 μV , SE = 0.28). No between-group difference was found in response to effortful movements ($p = 0.18$). A different modulation of the AN component was shown within each group of participants as a function of effort (see Fig 6 and 7). Specifically, the AN was more negative in response to effortful (-1.27 μV , SE = 0.32) than effortless (-0.83 μV , SE = 0.28) movements in controls ($p = 0.04$). The opposite effect was found in the brain of dancers ($p = 0.01$), which showed a larger negativity in response to effortless (-2.37 μV , SE = 0.28) than effortful movements (-1.85 μV , SE = 0.32).

A main effect of hemisphere [$F(1, 30) = 77.108, p < 0.001, \eta_p^2 = 0.36$] was also found. The negativity was larger over the left (-1.67 μV , SE = 0.21) than the right (-1.49 μV , SE = 0.19) hemisphere regardless of dance expertise.

Moreover, as shown by the significance of the electrode factor [$F(2, 60) = 9.288, p < 0.001, \eta_p^2 = 0.24$], the AN was more negative over the medial (Aff1-Aff2: -1.64 μV , SE = 0.21; FFC1h-FFC2h: -1.65 μV , SE = 0.21) than the lateral (F3-F4: -1.45 μV , SE = 0.19) electrode sites ($p < 0.001$).

Finally, the interaction between electrode and hemisphere factors [$F(1.29, 38.60) = 5.485, p < 0.02, \hat{\epsilon} = 0.64, \eta_p^2 = 0.15$] indicated that the negativity was larger over the left than the right hemisphere at lateral sites ($F3-F4: p < 0.001$), approached significance level at central sites ($FFC1h-FFC2h: p = 0.10$), but was absent at frontal sites ($Aff1-Aff2: p = 0.61$). Furthermore, the difference between medial and lateral sites (showed by the main effect of the electrode factor) was visible only over the right ($p < 0.001$) but not the left ($p = 0.94$) hemisphere.

3.2 SwLORETA source reconstruction (400-550 ms)

A swLORETA source reconstruction was performed for each group of participants to investigate the neural source of the potential recorded over the scalp. The swLORETA was applied to the difference wave obtained subtracting the ERP evoked by effortless steps from those elicited by effortful steps in the AN time window (400-550 ms). A list of the estimated active electromagnetic dipoles for dancers and controls is presented in Table 2. The main dipoles were located in the occipitotemporal cortex (BA 20/21, 37) in the brains of dancers, while the task-related frontal regions (BA 10, 11, 47) showed the larger magnitude in controls (see Fig 8). Temporal and limbic areas (BA 38, 28) were also active in both groups, being bilaterally engaged in dancers. Lastly, greater and bilateral engagement of frontoparietal visuomotor regions (BA 40, 6) was found in dancers relative to controls.

4. Discussion

The present study investigated the time course and neural correlates of action representation underlying kinesthetic motor imagery (KMI) of complex action (ballet movements). After practical MI (motor imagery) training, ballet dancers and controls were presented with videos depicting technical ballet movements varying in muscular effort requirements (effortful vs. effortless) and instructed to reproduce them mentally (see Fig 4). If specific motor knowledge was required for KMI, ballet dancers (vs. controls) would show increased frontoparietal activity, possibly associated with an enhanced recalling of kinematics and body-related information through visuomotor action simulation.

As can be appreciated in Fig 5, KMI of dance action resulted in a negative potential with a maximum peak amplitude over anterior scalp sites between 400-550 ms (Anterior Negativity,

AN). A fronto-central long-lasting negative potential has been previously shown during MI of repetitive movements (i.e., tennis ball throwing), with two maximum peaks around 300 ms and 1000 ms (Cebolla et al., 2015). Enhanced amplitude in frontal midline theta (4-7 Hz) frequency band has also been reported during the imagination of dart-throwing after MI training, interpreted as an index of improved allocation of attentional resources (Weber et al., 2016). The latter result is consistent with the location of the AN reported here, larger over the midline than lateral scalp sites but also more left distributed. The left asymmetry suggests the occurrence of kinesthetic (rather than visual) motor imagery processes (Guillot et al., 2009; Ptak et al., 2017) in all participants, as requested by the experimental task and experienced during the MI training phase. In this regard, a left-hemispheric dominance has been previously shown for fine motor control, planning, and imagination in both healthy participants (Kuhtz-Buschbeck et al., 2003; Olsson et al., 2008; Serrien et al., 2006) and clinical patients suffering from a left-hemispheric stroke (Sabaté et al., 2004; Yan et al., 2012). For instance, activity in the left dPM, vPM, and SMA has been reported during MI of finger movements of either hand regardless of task complexity (Kuhtz-Buschbeck et al., 2003).

In the present study, the AN was more negative in the group of dancers relative to controls, which suggests increased premotor processing of the mental image due to acquired motor knowledge of the ballet steps. Several fMRI studies have shown the enhanced engagement of prefrontal regions in expert athletes during MI of known technical actions (Chang et al., 2011; Cross et al., 2006; Wei and Luo, 2010). Bilateral SMA activity (greater on the left hemisphere) has been reported in elite archers during archery shot MI, contrarily to non-expert controls showing a broader recruitment of brain regions (i.e., SMA, pre-SMA, IPC, IFG, BG, and cerebellum; Chang et al., 2011). Enhanced engagement of the dorsolateral PM (along with SPL and occipital areas) has also been reported during pre-shot routine MI in expert golf players (Milton et al., 2007), while controls showed activity in subcortical (BG) and limbic (i.e., PCC) areas. These results suggest increased organization and efficiency in brain network underlying motor planning in experts, likely indicating a refined capability to integrate motor and sensory information. This evidence is also consistent with increased corticospinal excitability reported in expert tennis players during MI of practiced (relative to kinematically similar non-practiced) tool-related movements (Fourkas et al., 2008), suggesting a more sophisticated cortical representation of specific hand actions in experts, recalled during MI.

Of particular interest within the present study was the effort-related modulation of the AN as a function of dance expertise, with a larger AN response to MI of effortful (vs. effortless)

movements in controls (see Fig 6A and 7). This result possibly suggests increased cognitive demands in participants lacking in motor knowledge of the specific action. In this regard, increasing kinematic information has been previously associated with increased muscular effort information conveyed during action observation (Proverbio et al., 2009). Previous TMS studies have reported enhanced corticospinal excitability during MI of finger (Helm et al., 2015), wrist (Tatemoto et al., 2017), and foot (Kato et al., 2017) movements requiring increasing effort. Increased cognitive load has been previously reported during MI of ballet sequences relative to non-dance actions, as indexed by increased ERD in alpha and beta frequency bands (di Nota et al., 2017). The dancers showed an opposite pattern of results with reduced AN elicited by MI of effortful (vs. effortless) movements. In this regard, Pau and colleagues (2013) reported increased activity of visuomotor regions during the observation of piano finger movements in pianists (vs. controls), and subsequently decreased neural resources required by actual execution (“neural efficiency”). Since the partial functional overlap between the neural substrates that underlie MI and motor planning (Hardwick et al., 2017; Jeannerod, 1994; 2001), we interpreted the present findings consistent with Pau’s study. In a previous paper (Orlandi et al., 2020), we reported evidence of increased frontoparietal activity (larger frontal P300 and parietal Late Positivity components) during the observation of the effortful (vs. effortless) dance movements (used in the present study) in ballet dancers (vs. controls). It is, therefore, possible that effort information has been efficiently processed by dancers while observing the actions, resulting in reduced cognitive demands (smaller AN to effortful vs. effortless movements) during imagined motor execution.

This interpretation of our results seems to be supported by both the scalp distribution and source reconstruction (swLORETA) of the effort-related difference wave (DW: effortful *minus* effortless) in the AN time window (400-550 ms). As can be seen in Fig 6B, DW was cento-parietally distributed in dancers, but more frontally located in controls. Respectively, it likely suggests that MI led to enhanced visuomotor processes in ballet experts and increased working memory processes in controls.

The swLORETA estimated the main neural generators of the DW in the right fusiform (FG, BA 20), inferior/middle temporal gyrus (ITG/MTG, BA 20/21), and bilateral frontoparietal regions (BA 6, 40) in dancers. The main active dipoles were localized in the frontal regions (BA 10, 11, 47) in controls (see Fig 8), as visible in Table 2, reporting the complete lists of estimated dipoles. Greater engagement of the right FG has been previously shown during MI of repertoire specific action (i.e., diving) in expert divers, together with

activity in the left parahippocampal region (Wei & Lou, 2010). The occipitotemporal cortex (OTC) includes regions selectively activated by the body, face, and motion observation, that show sensitivity to action content (Ma et al., 2018; Tucciarelli et al., 2015). Enhanced activity in these regions has been linked to refined ability to use body information in action-outcome prediction (i.e., basket shots) in expert (relative non-expert) basketball players (Abreu et al., 2012). In the same study by Abreu and colleagues (2012), the engagement of the orbitofrontal cortex (OFC) in non-expert controls suggests high-order decision-making processes required to predict outcome. Increased recruitment of OFC (BA 10), cerebellum, and PCC (posterior cingulate cortex, BA 23) has also been found during MI in participants with poor (compared with good) imaginative capability (Guillot et al., 2008) and related to memory formation (Frey & Petides, 2002). Hence, activity in the OFC found here might indicate increased cognitive demands in controls to mentally simulate the unknown dance movements.

In all participants, the OTC (i.e., precuneus, BA 18; FG, BA 37, ITG/MTG, BA 20/21) and left uncus/STG (BA 28/38) played a role in MI of complex action. Activity in the latter region has been reported during MI of finger movements (Burianová et al., 2013), repertoire specific actions (Wei & Luo, 2010), and also for recalling of consolidated autobiographical memories and natural scenes (Zeidman et al., 2015; Zeidman & Maguire, 2016). Here, the dancers exhibited bilateral recruitment of the uncus/STG along with the right PCC, regions that are part of the limbic system, and have been linked to an emotional response to the human body (Proverbio et al., 2014; Vocks et al., 2010). Enhanced activity in the PCC has been found in locomotor MI (Malouin et al., 2003) and linked to spatial attention (Mesulam et al., 2001).

Finally, another expertise-related difference concerned the recruitment of sensorimotor regions (BA 6, 40) that were right localized in controls but bilaterally engaged in dancers (i.e., left precentral gyrus, BA 6; right IPL, BA 40). A large amount of evidence has shown the role of the premotor and parietal cortex during MI (Héту et al., 2013; Pilgramm et al., 2016; Ptak et al., 2017), with increased activity in response to trained (relative to untrained) movements (Bar & DeSouza, 2016; Cross et al., 2006). For instance, Pilgramm and colleagues (2016) used multivariate pattern analysis (MVPA) to investigate brain regions engaged during MI of different hand actions (force production, pointing, extension-flexion). The pattern of activity that differentiated the actions was visible within the motor (left M1), premotor (left PM) and posterior parietal (left IPS, right IPL, SPL) regions, but also in LOTC (MT and EBA) and early visual cortex. These results suggested that these brain areas played a key role in the cognitive representation of the motor content during MI. Moreover, the engagement of PPC, SMA, and

PM has been linked to motor awareness and conscious intention (Desmurget & Sirigu, 2009; Desmurget et al., 2009), with activity in the left PPC (BA 40) modulated by MI training (Lebon et al., 2018; Olsson et al., 2008). Finally, enhanced activity in frontoparietal and cerebellar regions has been repeatedly reported in action anticipation tasks as a function of participants' increased visuomotor experience (i.e., sports practice) with the observed action (Blaser et al., 2014; Wright et al., 2013).

Overall, these pieces of evidence suggest different cognitive demands during kinesthetic motor imagery of complex dance action as a function of dance expertise. Increased cognitive load in controls was likely the result of the need to codify, remember, and recall a greater amount of effortful-related kinematic information. Contrarily, enhanced OTC, PM, and IPL activity in dancers associated with imagined effort information might suggest a more efficient retrieval of proprioceptive and sensorimotor information through action simulation.

A potential factor that might limit the conclusions of the present study could be the fact that the EEG/ERP technique is characterized by a high temporal (ms) but a non-ideal spatial resolution (Zani & Proverbio, 2003) when compared with functional imaging (i.e., fMRI, PET). However, several investigations have shown that the employment of a high-density EEG cap (i.e., 128 electrodes) together with advanced source reconstruction methods (i.e., swLORETA) lead to spatial resolution improvement of the EEG (Boughariou et al., 2015; Cebolla et al., 2017; Palmero-Soler et al., 2007). Moreover, the consistency between the estimated dipoles in our study and brain activity reported in several fMRI investigations on MI indicated good reliability of our findings.

In conclusion, from a methodological perspective, ERP was shown to be a good technique for investigating kinesthetic motor imagery processes regarding complex action. In previous studies, EEG modulation (ERD and LRP) evoked by MI has been compared with that elicited by the real execution of simple and repetitive movement (Carrillo-de-la-Peña et al., 2006; Yi et al., 2013). The reproduction of whole-body complex action during EEG recording remains a challenge due to motion artifacts (Urigüen & Garcia-Zapirain, 2015), even if successful methods for artifact removal have been recently demonstrated for locomotion tasks (Nathan & Contreras-Vidal, 2015). Here, the comparison between participants that varied in expertise regarding the specific repertoire of movement (ballet) allowed the identification of a common electrophysiological marker for kinesthetic motor imagery of complex action. Anterior Negativity (AN) response (400-550 ms) was elicited in all participants during the MI of technical dance movements, and its amplitude was modulated as a function of dance

expertise. The enhanced negativity found in dancers relative to controls was likely due to acquired motor knowledge with the specific movements. Moreover, MI of effortful movements was associated with increased AN and recruitment of prefrontal areas in controls, and with reduced AN in dancers, together with the engagement of (body-related) occipitotemporal and sensorimotor regions. This evidence seems to suggest reduced cognitive demands accompanied by enhanced simulation processes as a function of acquired expertise with the imagined action. Hence, we speculated that professional dance practice might have led to an enriched and refined representation of dance movements recalled during the mental simulation.

The present results could be of benefit within clinical frameworks. MI has proven to be a good complementary tool in physical rehabilitation therapy (Dickstein & Deutsch, 2007), as in the case of post-stroke (De Vries & Mulder, 2007) and Parkinson's disease (Caligiore et al., 2017). For instance, the AN might be used as an electrophysiological marker to assess the consolidation of action cortical representations (i.e., visuomotor simulation processes) in a pre/post-intervention context and test the efficacy of the treatment.

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Figure and Table Captions

Table 1. Demographic information of participants. Table reporting age, years of education, and expertise with dance for both groups of participants. Formal education (study level), the age of acquisition, dance training, professional, and teaching activity are expressed in years.

Table 2. Active electromagnetic dipoles list. List of active electromagnetic dipoles explaining the surface difference potentials (ERPs elicited by effortless stimuli subtracted from those elicited by effortful stimuli) recorded in dancers and controls according to swLORETA in the Anterior Negativity time window (400-550 ms), with the relative Talairach coordinates. The strongest sources of activation included the fusiform gyrus and inferior/middle temporal gyrus in dancers (BA 20/21). The main dipoles were instead located in the prefrontal areas in controls (BA 10, 47, 11). Limbic/associative regions (BA 38, 28) were bilaterally active in dancers and left lateralized in controls. Sensorimotor areas (BA 40, 6) were right localized in controls and bilaterally engaged in dancers. (Legend: Magn - magnitude, Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann area, FG- fusiform gyrus, ITG – inferior temporal gyrus, MTG – middle temporal gyrus, STG – superior temporal gyrus, CG – cingulate gyrus, MFG – middle frontal gyrus, SFG – superior frontal gyrus, IPL – inferior parietal lobule, MedFG – medial frontal gyrus, MOG – middle occipital gyrus)

Fig 1. Example of stimuli. Eight static frames have been taken from the relative videos representing effortful (left column) and effortless (right column) dance steps. The moment of the maximum peak of effort (synchronized at 1000 ms, 25° frame) is visible in each static frame. (double column)

Fig 2. Effort ratings from stimuli validation. Rating values of the perceived effort during the validation of the stimuli (effortful vs. effortless). The dancer (in grey) and control (in green) judges rated each stimulus as effortful (1) or effortless (0). The controls (compared with the dancers) seemed to underestimate the real effort required to reproduce the effortful movements. (single column)

Fig 3. Time scale of the motor imagery training. The participants were engaged in motor imagery (MI) training to acquaint with the MI task. The experimenter performed a series of movements in front of them coming from both daily-life (i.e., jump forward) and technical ballet repertoire (i.e., *échappé*). Firstly, the participants were instructed to observe and reproduce the movement (task 1). Secondly, they had to observe, reproduce, and imagine executing the movement (task 2). During the imagination phase, they were encouraged to recall the body-related sensation occurred during actual action reproduction. Thirdly, they were asked to observe and directly imagine executing the movement (task 3). (double column)

Fig 4. Time scale of the experimental design. Each trial consisted of the presentation of a videoclip (2000 ms) at the center of the screen followed by a red fixation cross on an isoluminant light grey background. The cross turned to blue after 900 ± 100 ms (interstimulus interval, ISI) and remained visible for 3000 ms. The participants were invited to observe each videoclip and kinematically imagine reproducing the dance step without any real movement execution at the cross color change. (single column)

Fig 5. Grand average waveforms recorded over the scalp. Grand average waveforms (ERPs) recorded over the entire scalp (128 electrodes) in dancers (in red) and controls (blue). A negative component was elicited by the imagination of the dance steps and maximum peaked over anterior sites. This Anterior Negativity was larger in the group of dancers relative to controls. The green shaded area highlights the selected time window (400-550 ms) and the specific electrode sites in which the mean area voltage was quantified. Mean amplitude values (μV) of the AN recorded at frontal sites as a function of acquired dance expertise (dancers vs. controls) are visible in the boxplots in the upper-left corner of the figure. (double column)

Fig 6. Grand average waveforms recorded at anterior sites. The upper part of figure (A) illustrates the grand average waveforms (ERPs) recorded over frontal sites in dancers (in red) and controls (in blue). The solid lines refer to the ERPs elicited by effortful movements, while the dotted lines refer to those elicited by effortless movements. The green shaded area highlights the selected time window (400-550 ms) in which the mean area voltage was quantified. The middle part of figure (B) shows the topographic maps of scalp voltage distribution of the difference wave (DW: *effortful-minus-effortless*) relative to AN temporal window (400-550 ms) in dancers (on the left) and controls (on the right). The positive values (in red) in dancers and the negative values (in blue) in controls reflect the opposite pattern of results as a function of the motor content (effort) in the two groups. The lower part of figure (C) illustrates the grand averages DWs obtained subtracting ERPs to effortful minus ERPs to effortless stimuli in the dancers (in red) and controls (in blue). (double column)

Fig 7. Amplitude values of AN component as a function of group and effort. The figure illustrates the mean amplitude values of the AN component (400-550 ms) as a function of the group and action effort. The two groups of participants showed an opposite pattern of results. Effortful (in green) relative to effortless (in grey) steps elicited larger negativity in controls. At the same time, the AN was more negative in response to effortless (compared with effortful) steps in dancers. (single column)

Fig 8. SwLORETA source reconstruction of surface potentials in the AN time window (400-550 ms). SwLORETA performed on the difference wave obtained by subtracting the ERPs elicited by effortless stimuli from those elicited by effortful stimuli (in the AN time window 400-550 ms) in dancers (on the left) and controls (on the right). The coronal, axial and sagittal anatomical planes of the brain are shown. The activation of the right fusiform gyrus (FG, BA 20) and bilateral inferior/middle temporal gyrus (ITG/MTG, BA 20/21) is visible in the brain of dancers. The activation of the right superior (SFG) and middle frontal gyri (MFG, BA 10) in the brain of the controls can also be appreciated. The strongest magnitude values of the signal (nAm) are shown in red. (double column)

Supplementary Material

Supplementary Table 1. List of movements. The table illustrates the list of technical gestures recorded from the six professional dancers on the basis of the muscular effort required to reproduce them. Effortless movements are reported in the left column; effortful movements are reported in the right column.

Supplementary Video 1. Examples of ballet movements. The video illustrates a few examples of effortless and effortful ballet steps used in the present study. Each stimulus lasted 2000 ms and displayed the maximum peak of effort at 1000 ms.