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ACTION REPRESENTATION IN THE HUMAN BRAIN: ELECTROPHYSIOLOGICAL MARKERS AND NEUROFUNCTIONAL CORRELATES

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Abstract

The present thesis aimed to investigate the time course and the neural substrates of body recognition and action representation using electrophysiological and neuroimaging studies. Previous evidence has shown that the presentation of a body in upside-down orientation resulted in decreased discrimination ability and increased N190 component, suggesting a disruption of configurational processing. In this thesis, the relationship between body recognition, orientation, and attention was assessed by presenting the participants with body postures and structures of cubes in either upright or inverted orientation. We predicted an effect of inversion on the perception of bodies but not cubes. The body inversion led to a slower stimulus processing (slower anterior N2) and enhanced attention allocation (larger Selection Negativity and P300) required to recognize and classify the target. Stronger recruitment of attention-related prefrontal regions was also found using swLORETA source reconstruction. No modulation of these components was shown for the cubes due to the lack of natural orientation. This first experiment provided evidence for an orientation-dependent recognition of the human body.

Several studies have found the engagement of fronto-parieto-temporal regions in action perception, modulated as a function of expertise. Here, a dancer's muscular effort was used as a tool to investigate the impact of ballet expertise on action representation. Compared to controls, a more refined and automatic effort encoding was expected in dancers due to their increased expertise with the repertoire of movement. Expert dancers and non-dancers were presented with effortful and effortless technical gestures and instructed to reproduce each of them mentally. A faster stimulus processing (faster posterior P2) and early bilateral engagement of the occipito-temporal cortex (OTC; posterior N2 and swLORETA) was found in dancers vs. controls during action observation. The experts also showed an increased anterior P300 and parietal Late Positivity (LP) in response to effortful than effortless steps. This was interpreted as an index of refined action coding due to their acquired motor knowledge. The non-experts only showed a modulation of the occipital LP likely due to enhanced processing of dance kinematics. The swLORETA indicated the recruitment of visuomotor regions in dancers, and visual and prefrontal areas in controls. During the motor imagery task a larger Anterior Negativity (AN) was found in experts compared to non-experts. Also, the effortful (vs. effortless) steps elicited a more negative AN in controls, while the opposite effect was found in ballet dancers. The swLORETA indicated bilateral recruitment of visuomotor and temporal areas in dancers and superior and medial frontal regions in controls. The evidence from the second study suggested a strong role of expertise in the modulation of the neural processes underlying action representation and an expertise-dependent contribution of the OTC to action coding during both observation and motor imagery.

The final study of this thesis explored the neural correlates of action timing representation. The volunteers judged the aesthetical appraisal of videos depicting dance sequences reproduced with a uniform or varied acceleration, showing a preference for the varied version. Enhanced activity within OTC and fronto-central regions was expected as a function of increased acceleration changes. We found that the varied (vs. uniform) version of the sequences engaged a broader network of areas cortical and subcortical areas. The OTC, premotor and supplementary motor areas, inferior parietal lobule, inferior frontal gyrus, insula, thalamus, and putamen exhibited a crucial role in the representation of action timing. These results suggest a strong embodied response during the processing of dance kinematics as a function of time variation.

List of abbreviations

ACC – Anterior cingulate cortex
AN – Anterior negativity
ANS – Autonomic nervous system
AON – Action observation network
AP – Arterial pressure
aPFC – Anterior prefrontal cortex
BA – Brodmann area
BG – Basal ganglia
BIE – Body inversion effect
BOLD – Blood oxygenation level dependent
CC- Corpus callosum
DLPFC – Dorsolateral prefrontal cortex
DTF – Direct transfer function
DTI – Diffusion tensor imaging
DW – Different wave
EBA – Extrastriate body area
EEG – Electroencephalography
EIP – Extensor indicis proprius
EPI – Echo-planar imaging
ERD – Event-related desynchronization
ERP – Event-related potential
ERN – Error-related negativity
FA – Fractional anisotropy
FBA – Fusiform body area
FDI – First dorsal interosseous
FDR – false discovery rate
FG – Fusiform gyrus
FFA – Fusiform face area
fL – Foot-lambert
fMRI – Functional magnetic resonance imaging
GLM – General linear model
GM – Grey matter
HERA – Hemispheric encoding/retrieval asymmetry
hMT+ – Human middle temporal
IFG – Inferior frontal gyrus
iLFP – Intractianial local field potentials
IPC – Inferior parietal cortex
IPL – Inferior parietal lobule
IPS – Inferior parietal sulcus
ISI – Inter-stimulus interval
ITG – Inferior temporal gyrus
KMI – Kinesthetic motor imagery
LOC – Lateral occipital cortex

LOTC – Lateral occipito-temporal cortex
LP – Late positivity
LRP – Lateralized readiness potential
M1 – Primary motor cortex
ME – Motion energy
MEG – Magnetoencephalography
MEP – Motor evoked potential
MI – Motor imagery
MNI – Montreal neurological institute
MNS – Mirror neuron system
MOG – Middle occipital gyrus
MT – Middle temporal
MTG – Middle temporal gyrus
MVPA – Multivoxel pattern analysis
OFA – Occipital face area
OFC – Orbitofrontal cortrex
OTC – Occipito-temporal cortex
PFC – Prefrontal cortex
PM – Premotor cortex
PPC – Posterior parietal cortex
RT – Reaction time
RSA – Representational similarity analysis
S1 – Primary somatosensory cortex
SD – Standard deviation
SE – Standard error
SFG – Superior frontal gyrus
SMA – Supplemental motor area
SN – Selection negativity
SOG – Superior occipital gyrus
SPC – Superior parietal cortex
SPL – Superior parietal lobule
STG – Superior temporal gyrus
STS – Superior temporal sulcus
SW – Slow wave
swLORETA – Standardized weighted low-resolution electromagnetic tomography
TE – Echo time
TMS - Transcranial magnetic stimulation
TOJ – Temporo-occipital junction
TPJ – Temporo-parietal junction
TR – Repetition time
V1 – Primary visual cortex
VLPFC – Ventrolateral prefrontal cortex
VMI – Visual motor imagery
vPM – Ventral premotor cortex
WM – White matter

Chapter 1

General introduction

«She writes things with her movements that I

for the life of me could never write with a pen»

Christopher Poindexter

1.1. Action representation

The first chapter of this thesis aims to introduce the theoretical reference framework explaining how actions are represented in the human brain. In the initial sections, specific emphasis will be placed on the neural substrates and temporal dynamics that underpin action coding and recognition (e.g., Action Observation Network, fronto-parietal system, mirror neurons) from both functional neuroimaging and electrophysiological perspective. This will be followed by a brief overview of theories and cognitive models on action understanding proposed during the last decades. Commonalities and differences between observation and motor imagination processes will also be discussed. Furthermore, particular relevance to the contribution of the occipito-temporal cortex in body and action perception will be highlighted. Instead, the last sections of this chapter will be focused on acquired visuomotor expertise and its role in modulating action processing. Evidence from studies involving professional athletes, musicians and, especially dancers, will be used to demonstrate the degree of refinement and automatism that action representation-related brain networks can achieve.

1.1.1. The neural substrates of action observation processes

The observation of an action performed by another person engages a broad network of cortical regions in our brain that encompasses frontal, parietal and occipito-temporal areas (Hardwick et al., 2017). This cluster of regions is usually referred to as Action Observation Network (AON) and has drawn growing attention of the neuroscientists over the last decades (Bonini et al., 2016). Specifically, a set of core visuomotor regions can be identified in the AON, along with several associative visual areas in the occipito-temporal cortex (OTC), active during action perception (see Figure 1.1 for a schematic representation of the AON). A number of evidence has shown recruitment of the premotor cortex (PM; Rizzolatti et al., 2002), inferior frontal gyrus (IFG; Kilner et al., 2009), inferior parietal lobule (IPL; Culham and Valyear, 2006) and the posterior part of the superior temporal sulcus (pSTS) during both observation and execution of a movement (Binder et al., 2017; Casper et al., 2010; Cattaneo and Rizzolatti, 2009). Namely, a portion of the neurons of these regions showed visuomotor proprieties, firing when the same movement was performed and perceived. Neurons with similar characteristic were previously identified in the ventral premotor cortex (F5 area) of the brain of the rhesus monkey and indicated as mirror neurons (Bonini et al., 2014; Di Pellegrino et al., 1992; Gallese et al., 1996). For this reason, this set of visuomotor regions in the human

AON is also referred to as human mirror neuron system or fronto-parietal system (Gazzola and Keysers, 2008; Rizzolatti and Sinigaglia, 2010; 2016). During the observation of action, the relative motor act would be internally simulated by the motor system of the observer without the production of any real movement. According to this theory, the neural representation of the action would "resonate" and be recalled in the brain of the observer (Grafton et al., 2009; Kilner et al., 2007). This coupling between production and observation would play an important role in action understanding, movement prediction, inference of the agent's goals and intentions, not to mention the acquisition of social-cognitive abilities such as empathy and language (Catmur et al. 2015; Iacoboni et al., 2005). This idea was also strengthened by growing evidence showing enhanced activity in the AON as a function of increased familiarity or acquired expertise with the observed repertoire of movement (Buccino et al., 2001; Kirsch et al., 2015).

In addition, several cortical regions have been found in the OTC whose activity is selectively evoked by body, face and motion perception. Especially, the extrastriate (EBA) and fusiform (FBA) body areas (De Gelder et al., 2015; Peelen and Downing, 2007) are generally engaged during the observation of human body or body-parts, while the occipital (OFA) and fusiform (FFA) face areas (Haxby et al., 2010; Rossion, 2014) are recruited by face processing. Finally, the human motion-selective complex (hMT+; Grossman et al., 2006), partially overlapping with the EBA, is known as multimodal motion processing area, being selectively activated by visual but also tactile motion patterns (Ricciardi et al., 2013; van Kemenade et al., 2014). Studies involving point-light animation (Grossman et al., 2000; 2010) also showed the selective response of the pSTS to biological motion (i.e., a man walking) when compared with non-biological motion (scrambled animation). A recent investigation involving multivoxel pattern analysis (MVPA) showed movement-specific representation (i.e., walk, run, jump, skip) in the EBA, hMT+, and pSTS (Ma et al., 2018). Functional connectivity with EBA was also shown in several regions of AON, including the IFG, IPL, precentral gyrus, MTG (middle temporal gyrus), STG (superior temporal gyrus), lateral OTC, precuneus, and cerebellum. Overall, these results were consistent with the idea of an early role of the OTC in processing information about human motion, that would be subsequently integrated into a broader network.

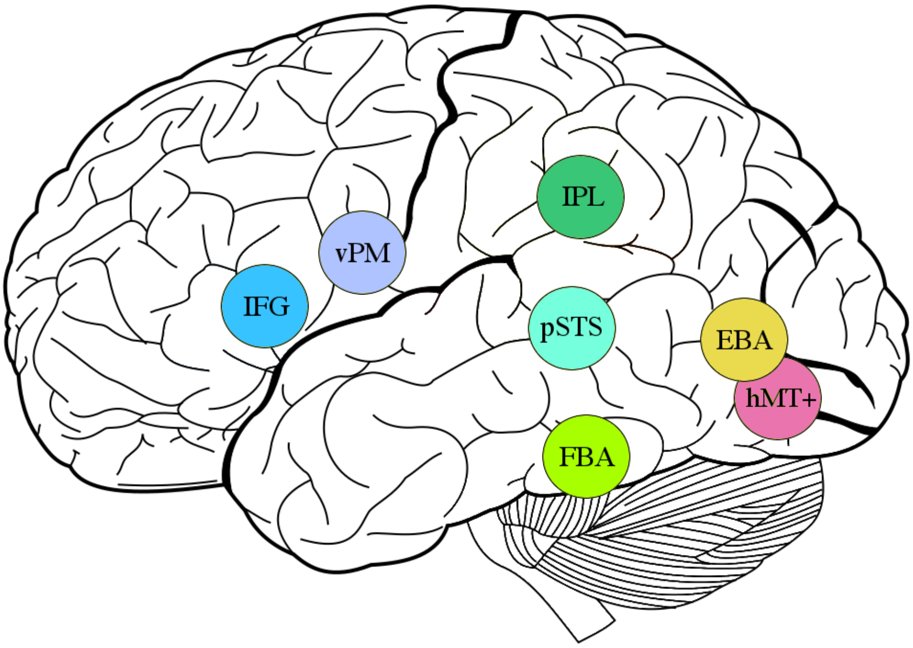


Figure 1.1. Schematic representation of the Action Observation Network (AON). The figure illustrates the brain regions that constitute the Action Observation Network (AON), including: the inferior frontal gyrus (IFG), ventral premotor cortex (vPM), inferior parietal lobule (IPL), posterior part of the superior temporal sulcus (pSTS), extrastriate body area (EBA), fusiform body area (FBA), and human motion-selective complex (hMT+).

In this regard, whether activity in the AON during action observation is widely supported, the specific role of each area within this network in action encoding is still subject to debate. One attempt to describe the organization and structure of the AON was provided by a series of fMRI studies by Grafton and Hamilton (2007). The authors used a repetition suppression approach to show a preferential engagement of different regions of the AON in the processing of different aspects of goal-oriented behavior (i.e., kinematics, goal-object, outcome). For instance, low-level kinematic information (i.e., hand trajectory, grip configuration, object movement) were localized in the inferior occipital cortex and posterior superior parietal cortex. The left anterior intraparietal sulcus and vPM were modulated by object-directed action goals, while outcome coding recruited the IPL bilaterally and right vPM (Hamilton and Grafton, 2006; 2007). Thus, the authors proposed action representation as hierarchically and functionally organized processes distributed over interconnected cortical areas. Importantly, they pointed out that these regions would likely be engaged in cascade processes rather than singularly contributing to a single aspect of action representation. This view would take account studies that provided different results, such as the engagement of left frontal (Casile et al., 2009) and posterior parietal (Costantini et al., 2005) regions in processing kinematic information (i.e., violation of two-third law, physically impossible vs. possible movements).

More recently, Handjaras and colleagues (2015) introduced the concept of action topography that, to some extent, assimilated the points of view of the different authors presented so far (Grafton and Hamilton, 2007; Rizzolatti et al., 2001). Namely, different categories of action would be coded in a distinctive but distributed and overlapped pattern of cortical regions functionally organized, subserving higher-level and more abstract representation. MVPA was used to investigate the ability of the AON to discriminate between transitive (i.e., grasping), intransitive (i.e., thumb up) and tool-mediated (i.e., sawing) actions (see the upper part of Figure 1.2). The three-way classifier showed discrimination ability within bilateral AON, including inferior and middle frontal regions, ventral and dorsal PM, IPL, SPL, LO, and ventral temporal regions. At the same time, specific areas were maximally informative for each action category. For instance, left prefrontal regions, anterior supramarginal, and postcentral gyri discriminated tool-mediated actions, while SPL, inferior occipital and right precentral cortex were informative for transitive actions. This idea of organized topographical representation was consistent with previous evidence by Ricciardi and colleagues (2013), that showed the existence of a supramodal and distributed action representation within the AON. In that study, blind and sighted participants were presented with audio and video stimuli representing hand-made actions and non-actions (environmental stimuli) during fMRI scanning. The classifiers (MPVA) were able to discriminate actions vs. non-actions not only within condition and group but also across conditions and groups. In the latter case, discrimination ability was shown within the IPL, SPL, ventral and right dorsal PM, and MTG/STG.

The debate on action representation is far from being solved since evidence provided by different authors are not always consistent. For instance, contrasting results have been reported on the role of the vPM in action representation at an abstract level. While some authors claimed the involvement of premotor regions together with the OTC and IPL (Hafri et al., 2017), others showed contravening evidence (Wurm and Lignau, 2015). In some cases, some methodological difference between investigations, such as the definition of the object of study, might account for the discrepancy in the results. In the above example, “action” was defined in terms of object state changes (i.e., open vs. close) by one research groups, while a definition based on the physical manner of interaction (i.e., kick vs. pull) was proposed by the other group of authors.

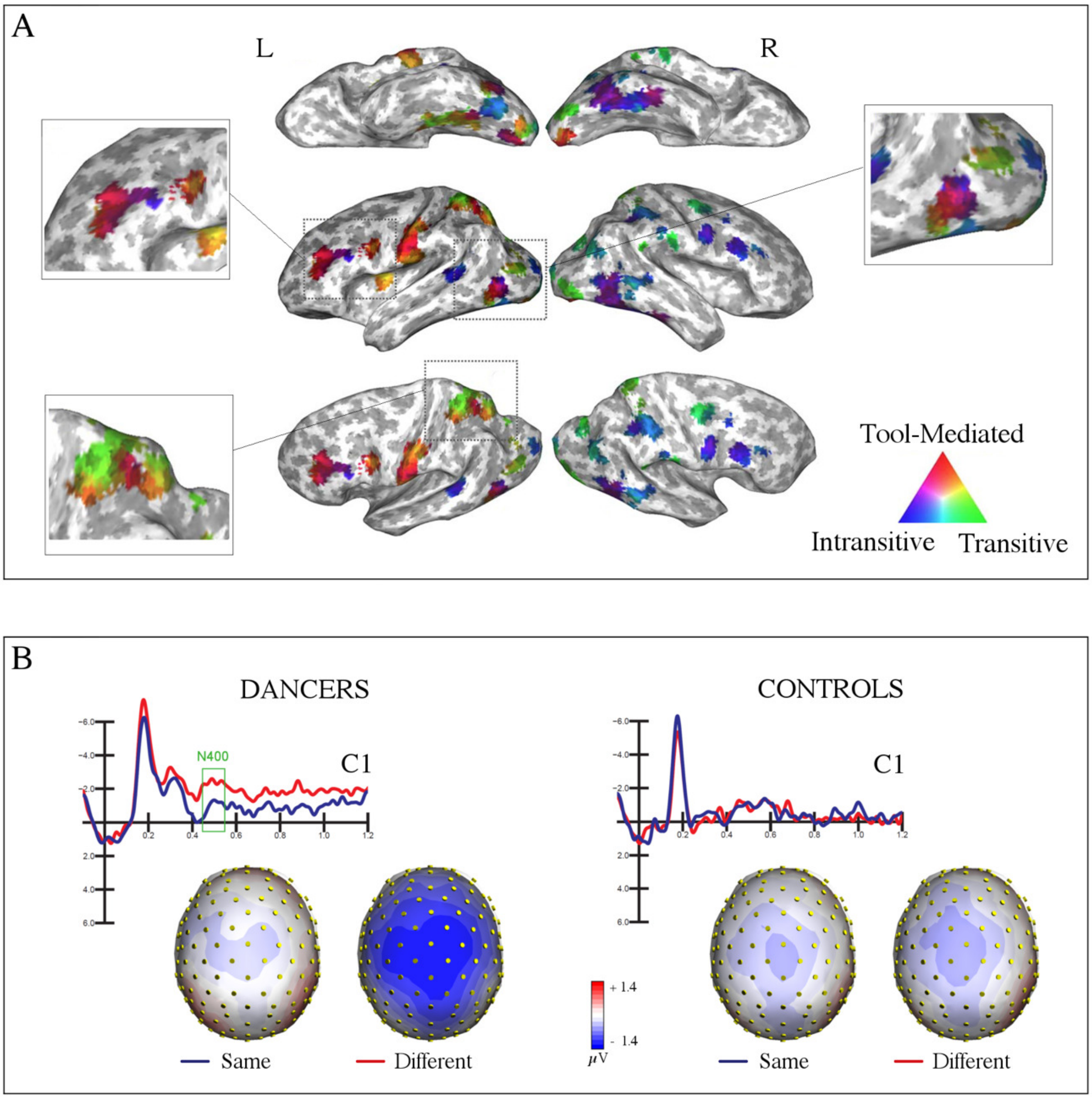


Figure 1.2. Examples of AON engagement during action observation. The upper part of the figure (A) displays the action-selective network, it is an adapted version of the original fMRI study by Handjaras and colleagues (2015). It shows a pattern of brain activity described by the three-way classifier that discriminated between transitive (green), intransitive (blue), and tool-mediated (red) action. The lower part of the figure (B) shows an example of ERP evoked during action observation, it is an adapted version of the original EEG study by Orlandi and colleagues (2017). It shows the grand-average wave forms recorded during the observation of same (in blue) and different (in red) video pairs in dancers and controls at central sites and the relative topographic maps of voltage distribution. In the dancers is visible a larger negativity (N400) elicited by different than same stimuli, suggesting a refined ability to automatically perceive small differences between movements due to acquired expertise.

From an electrophysiological perspective, neural markers and time courses of action observation-execution coupling have been investigated using both time-frequency analysis and event-related potential (ERP) technique. Specifically, the modulation of EEG rhythm in mu frequency band has been used and considered an index of the activity of the fronto-parietal system (Fox et al., 2016). Mu rhythm reflects the EEG frequency within the 8-13 Hz band and is recorded over central sites of the scalp (Pineda, 2005). Decreased in this specific frequency band is generally found during the execution of an action. Thus, the mu rhythm classically indexed an "idling” state of the sensorimotor areas. Similar amplitude reduction indicated as event-related desynchronization (ERD), was also observed when comparing EEG activity during action observation relative to a baseline period (Neuper et al., 2006). Change in mu rhythm has been found in response to grasping action and precision grip (Muthukumaraswamy et al., 2004a; 2004b), hand and foot movement (Pfurtscheller et al., 1997), oro-facial movement (Muthukumaraswamy et al., 2004c; Moore et al., 2012), but also complex whole-body movements (Orgs et al., 2008). Source reconstruction and EEG-fMRI coregistration studies localized the neural generator of this ERD modulation in the sensorimotor and parietal regions (Arnstein et al., 2011; Thorpe et al., 2015).

An example of ERD in mu band frequency has been provided by Cochin and colleagues (1999), that compared variation in EEG of volunteers during the observation and execution (vs. rest) of bimanual pincer movement (rhythmical thumb and index finger opposition). Reduction in the spectral alpha power (7.5-10.5 Hz) was found for both tasks over centroparietal, posterior frontal and temporal electrode sites. This result suggested that the same cortical areas were active while perceiving and reproducing a movement compared with resting. Subsequently, Muthukumaraswamy and colleagues (2004a) confirmed that mu rhythm (10-12 Hz) was strongly suppressed over sensorimotor regions while the participants were performing a precision grip compared to rest. During the observation of the same action, greater ERD was evoked when the precision grip was related to an external object rather than the same grip posture was shown without an object. These results corroborated the idea of execution-observation coupling and also suggested that greater engagement of this mechanism was triggered by the effector-object interaction. Evidence for mu band ERD elicited by graspable objects (i.e., tools) observation (vs. non-tools) suggested the recalling of grasping-related motor programs evoked by visual proprieties of the stimuli (Kumar et al., 2013; Proverbio, 2012). The mental simulation of action, including kinaesthetic motor imagery (Neuper et al., 2005; Pfurtscheller et al., 2006) and action outcome anticipation (Babiloni et al., 2010) also resulted in similar ERD.

Finally, event-related potentials (ERP) have been used to investigate the time course of action perception and representation. In this regard, the N400 and Late Positivity (LP) components have been reported as index of perceived incongruency (Proverbio and Riva, 2009; Giglio et al., 2013), variation (Orlandi et al., 2017) or error (Amoruso et al., 2014) in depicted action execution. For instance, Proverbio and Riva (2009) found that images representing complex actions violating the common word-knowledge (i.e., a girl sewing her hair) elicited a negativity between 350 and 500 ms (N400) over the anterior sites of the scalp when compared with congruent actions (i.e., a young woman driving a car). This was likely the result of a difficulty in understanding other's intentions or integrating present with previous knowledge. Similarly, an enhanced anterior negativity (N400) and posterior positivity (LP) was shown during the observation of actions ending in an unexpected way (Giglio et al., 2013) or that were incongruent with the context (Sitnikova et al., 2003; 2008). Orlandi and colleagues (2017) showed an enhanced sensitivity of these two components to the motor content of the stimuli as a function of increased motor experience. The automatic detection of subtle kinematic variations between video pairs representing complex whole-body actions resulted in fronto-central N400-effect and reduction of LP in expert dancers but not controls (see the lower part of Figure 1.2). These results suggested refined and specialized action representation processes as a consequence of extended and intense visuomotor practice. Overall, these pieces of evidence show that not only mu ERD but also ERP components can be a useful technique to investigate cognitive movement representation. ERP classically associated with the semantic analysis in studies about language (i.e., N400) can be extended and used to study sensorimotor processing and action representation.

1.1.2. Theories and role models of action understanding

Understanding the intentions underneath the actions of other individuals plays an important role in our daily social interaction and development of socio-cognitive functions (i.e., language, empathy). Thus, it is not surprising that several models and theories have been proposed trying to conceptualize cognitive and neural mechanisms underlying action understanding. As discussed in the review paper by Rizzolatti and colleagues (2001), different evidence coming from human and primates' studies and gathered at the beginning of the last decade corroborated two main hypotheses. A first perspective was referred to as visual hypothesis and claimed that the visual analysis and integration of a number of elements implied in action would be at the root of others' intention understanding (Perret et al., 1990). This view was supported by a pattern of activity shown in a population of neurons in the anterior part of the STS in the brain of the monkey. These neurons were maximally firing when the agent was executing a reaching movement toward the monkey while paying attention to the arm. When the same movement was executed but with the eye gaze (attention) directed elsewhere, a significant reduction of activity was found. Thus, high-order visual neurons in this region seemed to be able to integrate information about the observed action with the direction of the attention of the agent (Jellema et al., 2000). This would allow inference about the intention of the individual moving.

An alternative proposal was the so-called direct-matching hypothesis, based on the discovery of bimodal mirror neurons in the ventral premotor cortex (F5 area) of the primates and homologs findings in the human brain (Rizzolatti et al., 2001). A network of visuomotor neurons (IFG, vPM, IPL, pSTS) would allow a mapping of the visual representation of the observed action onto the motor representation of the observer. The same brain regions engaged by action execution would also be active during the observation of the same motor act (Hardwick et al., 2017). Thus, action understanding would be the result of a simulation process based on the motor knowledge of the observer (Rizzolatti and Craighero, 2004). Extensive EEG (Babiloni et al., 2016), TMS (Fadiga et al., 1995) and imaging (Buccino et al., 2004) literature has provided evidence in favor of this action observation-execution coupling. Namely, the simulation theory is currently one of the most convincing theoretical frameworks for action understanding. It is considered a milestone for the studies on the development of empathic abilities, social cognition, and language acquisition (Gallese, 2001). This discovery also had a great clinical relevance. A limited evolution of this mirror system has been correlated with the occurrence of critical elements that characterized individual suffering from autism spectrum disorders (Rizzolatti et al., 2009).

The idea of visuomotor resonance through the activity of fronto-parietal regions has also led to a thorough debate that has not ended yet (Hickok, 2009; 2013; Caramazza et al., 2014). For instance, Hickok (2009) critically reviewed evidence in support of the mirror neurons and reported several issues against this position. In this context, further cognitive hypotheses have been proposed to explain action’s goal comprehension, supported by weaker evidence (Brass et al., 2007). For instance, the action-reconstruction account proposed by Csibra (2007; 2008) stated that intention understanding was the result of specialized inferential processes engaging brain areas with no mirror proprieties. Specifically, two factors could define the difference between this model and the simulation hypothesis: the interpretation level of action representation and the direction of activity propagation within the visuomotor system. Following the direct-matching hypothesis, low-level representation of action (i.e., kinematics) would resonate in the brain of the observer and a bottom-up propagation would allow goal understanding through motor simulation. Contrarily, the action-reconstruction account claimed that action is reconstructed starting from high-level representation (i.e., goals) and that top-down propagation would allow predictive emulation that generated the relative motor programs. The cognitive and simulation theories should not be mutually exclusive. Thus, resonation processes would explain the action goal in a stereotypic/high familiar context where no active inference was required. At the same time, inference-based processing would be required in a novel/unusual situation where the evaluation of the efficiency of the action according to it contextual constraints is needed.

Finally, an interesting predictive coding framework based on empirical Bayesian inference has been proposed by Kilner and colleagues (2007). Action understanding would be the result of a minimization process of prediction error through reciprocal interactions among levels of the cortical hierarchy (i.e., intention, goal, motor program, kinematics). Namely, predicted and observed kinematic parameters of a movement would be compared resulting in prediction error. This error would be used to update the action representation at a motor command level. Then, prediction error obtained by comparing internal and external motor command would be used in updating goal representation level. This perspective was corroborated by recent evidence showing modulation of the AON not only as a function of familiarity/expertise but also novelty (Cross et al., 2012; Liew et al., 2013). For instance, increased activity in premotor, parietal and occipito-temporal regions was shown during the observation of rigid robot-like movement than natural human motion, regardless of whether the agent was human or a robot (Cross et al., 2012). Thus, extremely familiar/known but also unfamiliar/unknown action resulted in an enhanced engagement of AON during action observation (Liew et al., 2013). This pattern of results that seemed to be in contrast with the classical resonance hypothesis was instead consistent with predictive coding perspective.

1.1.3. Action imagination

Valuable insights into action representation also came from studies on action imagination. As it will be presented in the present section of the chapter, motor imagery and action observation processes partially share overlapping neural substrates (Hardwick et al., 2017; Hétu et al., 2013). See Figure 1.3 (upper part) for an overview of brain regions engaged during motor simulation of an action. Motor imagery (MI) was classically defined as "a dynamic state during which a subject mentally simulates a given action" and "implies that the subject feels himself performing" that action (Decety, 1996). Namely, it is an action simulation process without any real movement execution. It is "part of a broader phenomenon of motor representation related to intending and preparing movements", as proposed by Jeannerod (1994; 2001). In this perspective, a motor image was intended as "a conscious motor representation". During the last decades, growing attention has been given to the relative cognitive mechanisms and used as support in sports practice (Ridderinkhof and Brass, 2015) and physical rehabilitation therapy (Dickstein and Deutsch, 2007). In this regard, Hanakawa (2016) has recently highlighted the complexity and heterogeneity of this mental ability, suggesting for instance that different cognitive processes may be involved as a function of the MI task, individual strategy, and consciousness. Thus, the author proposed several factors that may be helpful to organize the concept of MI and guide future investigations, that is, motor control, explicitness, sensory modalities, and agency.

A common distinction has been made between two types of MI processes (Annett, 1995): kinaesthetic motor imagery (KMI) and visual motor imagery (VMI). During KMI, an individual is generally asked to focus on the sensorimotor and bodily sensations occurred during the actual reproduction of the same action. Instead, VMI requires the imagination of the scene from a first-person (internal VMI) or third-person (external VMI) perspective. In the first case, the individual imagines watching thought his/her eyes, while in the second case he/she is looking at the self (Jiang et al., 2015). fMRI evidence suggested that these different cognitive processes relay on distinct but partially overlapping neural circuits (Guillot et al., 2009; 2014; Kilintary et al., 2016). For instance, Guillot and colleagues (2009) compared brain activity during KMI and VMI (vs. real execution) of a sequence of finger movements. KMI engaged the SMA (BA 6, anterior and posterior part), IPL (BA 40, lateral and anterior part), frontal areas (BA 9, 24, 44), bilateral basal ganglia (putamen and nucleus caudatus) and cerebellum. SMA (posterior and superior part) and IPL (posterior part) were also active during VMI, along with occipital visual (BA 17, 18, 19) and superior parietal regions (BA 5,7). These results suggested a recall of visual features during VMI, while motor simulation processes were involved in KMI of the action. This evidence was supported by a recent TMS study by Mizuguchi and colleagues (2017), that showed increased corticospinal excitability (larger MEPs) after the stimulation of M1 during both KMI and VMI of finger tapping. At the same time, an increased probability to observe phosphenes was found stimulating V1 during VMI but not KMI.

Moreover, the imagination ability of the participants has been linked to a different modulation of the brain network underlying KMI (vs. real execution). Guillot and colleagues (2008) compared skilled imaginers with un-skilled imaginers during KMI of finger movements. Enchained activity was found in the lateral PM (BA 6), IPL (BA 40), SPL (BA 7), left ACC (BA 24) and putamen. This was interpreted as an index of better motor representation created during early acquisition stage of the fingers sequence. Contrarily, the poor imagers showed specific engagement of the cerebellum, OFC (BA 10) and PCC (BA 23), regions related to memory formation. These results were also confirmed by Jiang and colleagues (2015) that compared KMI with both internal and external VMI while the participants imagined themselves "running up the stairs" in the three MI conditions. Common activity was found in the right SMA (BA 6) regardless of the MI modality, while the basal ganglia (caudate) bilaterally and left frontal regions (BA 45, 47) were active during KMI (vs. VMI). Whether both VMI modalities engaged areas within the ventral stream, internal (vs. external) imagery also engaged regions within the dorsal stream.

Modulation of the activity in the sensorimotor regions as a function of perceived imagery vividness has also been found by a parametric fMRI study (Lorey et al., 2011.) Increased perceived imagery vividness was related to enhanced activity in the left IPL, SPL, M1, S1, and PM, putamen, and cerebellum bilaterally. Thus, motor images relied on action representation located in the motor and motor-related regions, consistently with the simulation hypothesis by Jannerod (1994, 2001). Functional similarities between cognitive processes underlying MI and motor preparation for real action execution have been proposed (Ruffino et al., 2017). Converging evidence seemed to support this hypothesis. Mental chronometry studies (Munzert, 2008; Reed, 2002) showed a correspondence between actual and mental duration of an action (i.e., walking, writing, drawing). Mental rotation tasks involving body stimuli indicated the engagement of the precentral sulcus when a motor simulation strategy was used by the participants (Zacks, 2008). Moreover, an MVPA study (Oosterhof et al., 2012) identified the left anterior parietal cortex as a brain region specialized for action representation (i.e., lift vs. slap) generalized between execution and imagination. Several TMS studies showed enhanced corticospinal excitability (larger MEPs) during both real execution and MI of finger and foot movements, as a function of increasing muscular fatigue (Helm et al., 2015; Kato et al., 2017).

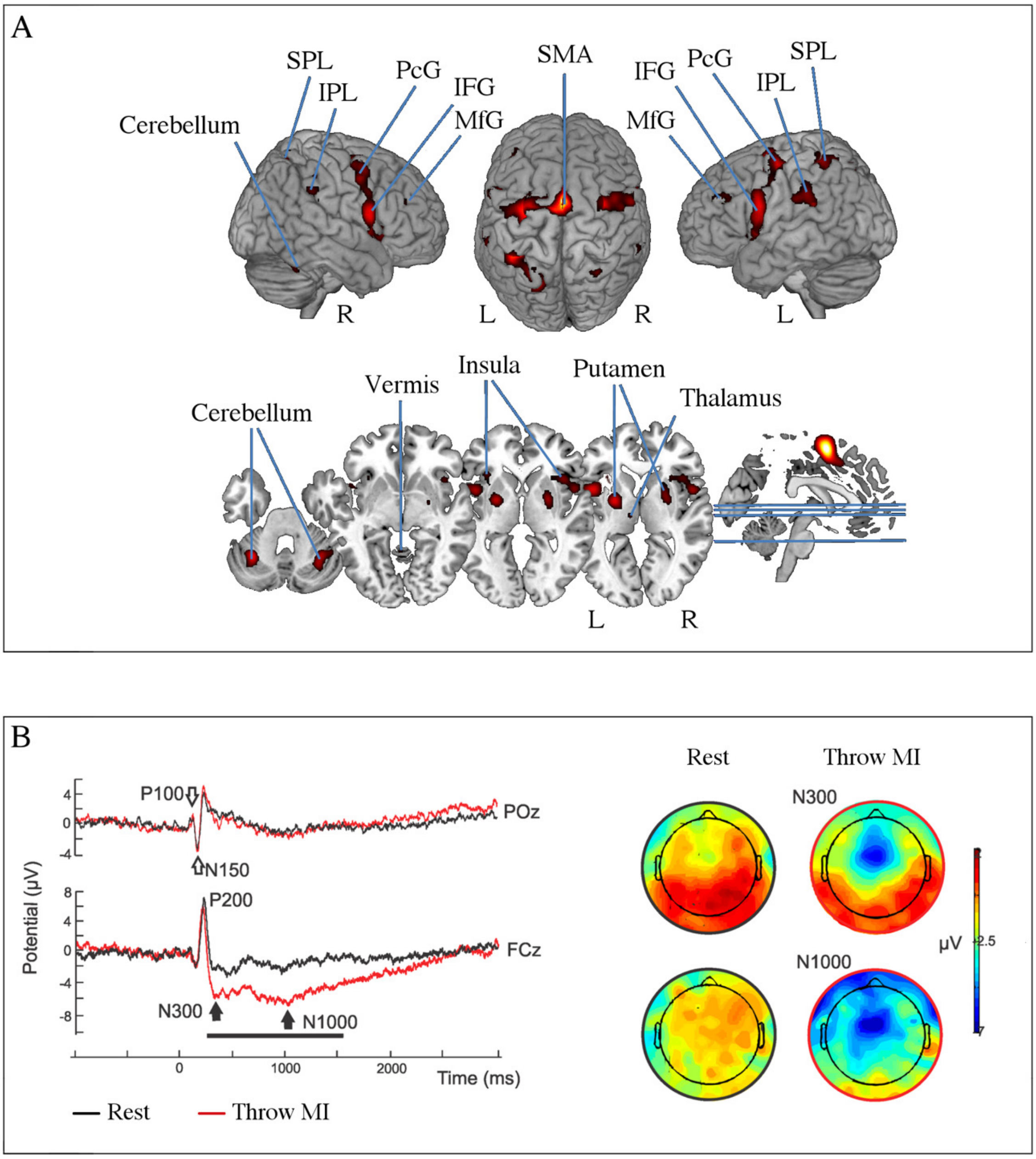


Figure 1.3. Examples of studies on motor imagery. The upper part of the figure (A) represents the neural substrates of motor imagery. The image is an adapted version of the original ALE meta-analysis by Hétu and colleagues (2013). Fronto-parietal and subcortical regions are shown. The lower part of the figure (B) shows the ERP evoked during a motor imagery task (in red) compared with rest (in black). The image is an adapted version of the original EEG study by Cebolla and colleagues (2015). It shows the grand-average wave forms recorded at posterior and fronto-central sites and the relative topographic map of voltage distribution. A larger N300 and N1000 is visible when the participants were imagining throwing a ball relative to a rest period.

A critical issue that is still subject to debate concerns the role of primary motor areas (M1) as crucial regions in MI processes (Munzert et al., 2009). Whether TMS (Loporto et al., 2011) and EEG (Neuper and Pfurtscheller, 2010) evidence seems to confirm recruitment of M1, two recent meta-analysis (imaging studies) showed consistent recruitment of these regions during action execution but not imagination (Hardwick et al., 2017; Hétu et al., 2013). For example, Carrillo-de-la-Peña and colleagues (2006) found similarities in lateralized readiness potentials (LRP) during imagined and executed hand and foot movements. LRP is an event-related component usually measured over C3 and C4 electrode sites, linked to the motor preparation and evoked by the activity of the primary motor cortex (Leuthold and Jentzsch, 2002). MI elicited LRP of similar latency and waveform to actual execution. Moreover, LRP related to foot movements exhibited opposite polarity than those related to hand movements in both conditions. These results suggested not only the recruitment of primary motor cortex during action simulation but also the same somatotopic organization of M1 in real and imagined execution (Ehrsson et al., 2003).

Together with LRP evidence, time-frequency analysis has shown a pattern of EEG modulation during MI that was similar to those related to real execution. A case in point was the EEG study by Pfurtscheller and colleagues (1997; 2001), by which an event-related desynchronization (ERD) in the mu rhythm (8-12 Hz) frequency band was found over contralateral sensorimotor regions during the imagination of unilateral hand movements. ERD in the beta rhythm frequency band (centered at 24 Hz) over the vertex was also shown during MI of left/right-hand movements (McFarland et al., 2000). This result was confirmed by single-trial MI classification study in which kinesthetic (KMI) and visuomotor (VMI) imagery was compared with execution and observation of right-hand movements (Neuper et al., 2005). The highest discrimination rate between KMI and rest was obtained over the contralateral (left) sensorimotor sites and based on ERD on mu (10-14 Hz) and beta rhythms. Further EEG-fMRI coregistration studies showed a negative correlation between alpha/beta ERD (i.e., 10-12 Hz, 13-30 Hz) and increased BOLD signal in contralateral sensorimotor regions and SMA during MI (Formaggio et al., 2010).

Somatotopic organized engagement of sensorimotor regions was also visible as a function of the body part involved in the movement (Yuan et al., 2010). For example, ERD in broader frequency bands (Yi et al., 2013) over central sites was shown when comparing MI of complex/compound limb movements (i.e., 8-11 Hz, 18-24 Hz) than simple/unilateral limb movements (i.e., 8-9 Hz). Moreover, several patterns of ERD and ERS (event-related synchronization) were found in different time-windows during MI of complex action (i.e., throwing a ball with the right hand) compared to rest (Cebolla et al., 2015). A contralateral mu ERD (9-13 Hz) was shown 500 ms after MI onset (530-750 ms), that was likely the result of the activity of sensorimotor regions. This was followed by increased synchrony (ERS) in theta frequency band (3-5 Hz) over fronto-central sites of the scalp (750-900 ms), interpreted as processes of attention allocation to target stimuli. Finally, ERD in high alpha/low beta (9-17 Hz) was shown over frontal and parieto-occipital regions (1000-1150 ms), respectively interpreted as an index of motor planning and proprioceptive/visual information processing (see the lower part of Figure 1.3). Overall, these pieces of evidence indicate a modulation of MI processes (Olsson and Nyberg, 2010) as a function of the body parts involved (Carrillo-de-la-Peña et al., 2006; Szameitat et al., 2007) and action complexity (Kuhtz-Buschbeck et al., 2003; Yi et al., 2013).

Finally, a specific modulation of action simulation has been found as a function of visuomotor expertise with the specific motor repertoire (Milton et al., 2007; Wei and Luo, 2010), as in the case of music (Lotze et al., 2013) and sports (Filgueiras et al., 2017; Milton et al., 2008) practice. For instance, an overall reduced brain volume activity during MI of pre-shot routine (preparation for the golf swing) was found in expert golf players than controls (Milton et al., 2007). Specifically, the SPL, lateral PM (dorsal) and occipital regions were more engaged in the experts, while limbic regions (PCC, amygdala-forebrain complex and BG) were recruited in non-experts only. These results suggested a more efficient neural network for specialized motor planning and visuomotor integration as a result of extended practice. At the same time, limbic activation in non-players was interpreted as difficulty in filtering irrelevant information due to lack of motor representation. Similarly, a comparison between expert and non-expert archers during archery shooting indicated the engagement of the SMA bilaterally with left dominance in archers and broader recruitment of brain regions in non-archers, that included the M1, PM, SMA, IPC, IFC, BG, and cerebellum (Chang et al., 2011). Whether intense training seemed to lead to a refined and organized neural network, individuals that were still in the process of motor learning needed extensive brain resources to imagine executing the action.

1.1.3. The role of the occipito-temporal cortex in body and action perception

The capability to perceive and recognize other individuals is crucial for social interactions and partially relies on the extrapolation and interpretation of face and body features (Minnebusch et al., 2009). Body posture can convey information on age, gender, emotional state (de Gelder et al., 2015), and intentions of others (Downing and Peelen, 2011; 2016). Over the last decades, different methodological studies provided converging evidence of cognitive processes and neural substrate of human body perception (de Gelder et al., 2010; Peelen and Downing, 2007). Several fMRI investigations showed a selective activation in the occipito-temporal cortex (OTC) in response to static and dynamic bodies or body parts when compared with faces, animals, and objects. Particularly, two regions within the extrastriate visual cortex (Downing et al., 2001) and the middle fusiform gyrus (Peelen and Downing, 2005; Schwarzlose et al., 2005) were identified and respectively referred to as extrastriate body area (EBA) and fusiform body area (FBA). Increased responses in these regions were found in response to images depicting real bodies, as well as silhouettes, line drawings, and stick figures (see the upper part of Figure 1.4).

Evidence from intracranial recording studies seemed to confirm the existence of these stimulus-selective regions in OTC (Engell et al., 2014; Pourtois et al., 2007). For instance, Pourtois and colleagues (2007) recorded intracranial local field potentials (iLFPs) in the right extrastriate cortex of an epileptic patient. A negative potential evoked by body stimuli (rather than faces, animals, and objects) was identified from 190 ms, and maximally peaking at 260 ms, at a specific electrode site compatible with EBA location. Electrophysiological investigations also showed that the observation of an intact (than scrambled) body elicited a negative potential at approximately 190 ms (N190 component) over occipito-temporal sites of the scalp (Thierry et al., 2006). See Figure 1.4 (lower part) for an example of the N190 component. This negativity was similar to the N170 component elicited by face perception at 170 ms (Rossion, 2014), even though it was later and dorsal distributed. These body- and face-related negative components are generally interpreted as an index of structural encoding of the visual stimulus. Further EEG and MEG (magnetoencephalography) evidence confirmed the EBA as the main neural generator of the N190. One example is the study by Taylor and colleagues (2010), in which the amplitude values of the N190 during the observation of body parts (including fingers, hands, arms, and torso) was compared with the hemodynamic activity in OTC evoked by the same stimuli in a previous fMRI study (Taylor et al., 2007). Another instance was provided by the MEG study by Ishizu and colleagues (2010), in which body observation led to an M190 component originated in the middle temporal gyrus (MTG), while an earlier M170 originated in the inferior temporal gyrus (ITG) was evoked by faces (Ishizu et al., 2010).

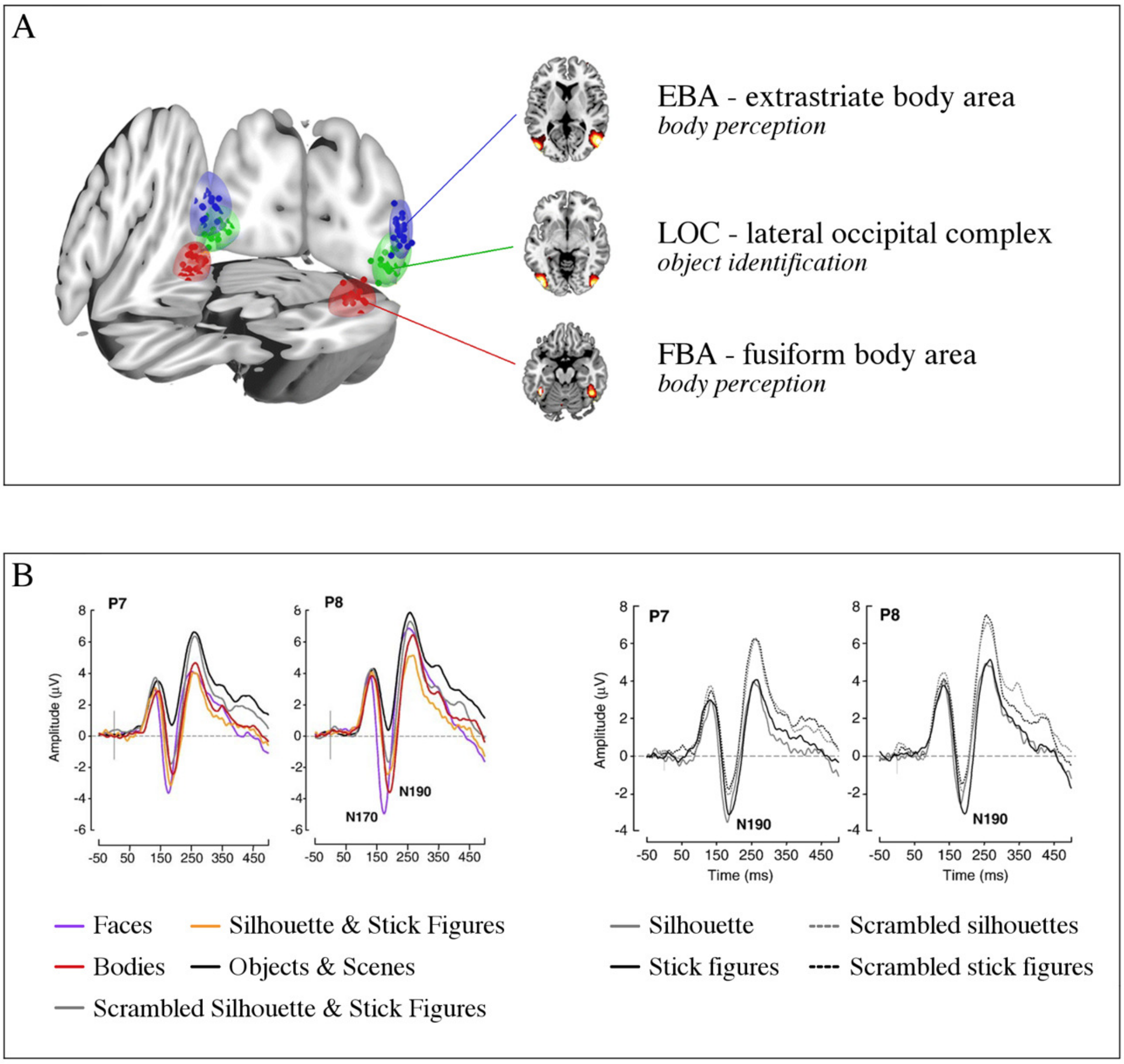


Figure 1.4. Examples of selective response of the occipito-temporal cortex to body perception. The upper part of the figure (A) displays the location the EBA (blue), FBA (red), and LOC (green). It is an adapted version of the original fMRI study by Zimmermann and colleagues (2018). The lower part of the figure (B) shows the grand-average wave forms recorded over posterior sites during the observation of different categories of stimuli. It is an adapted version of the original EEG study by Thierry and colleagues (2006). The N190 component is larger in response to bodies (in red) than objects and scenes (in black). The N170 component is larger in response to faces (in purple) than any other category.

Several pieces of evidence seemed to suggest a functional role of FBA in perceiving the body in a configurational way (Bernstein et al., 2014), while EBA would be involved in body parts processing (Moreau et al., 2017; Orlov et al., 2010). This difference resembles that proposed for face perception (Minnebusch et al., 2009), involving respectively the FFA and OFA (occipital face area). For instance, increased activity in FBA, but not EBA, was found (Taylor et al., 2007) with increasing amount of body parts shown (from fingers to torso). Also, TMS (transcranial magnetic stimulation) pulse delivered over EBA let to an impairment (increased reaction times) during body (vs. face) recognition (Urgesi et al., 2004) and reduce sensitivity to body aesthetic appreciation (Calvo-Merino, 2010). This issue has not been solved completely since opposing evidence has been provided. The study by Brandman and colleagues (2014) is a case in point, because they showed an increase response also in EBA to whole bodies, rather than same body parts when presented in a different configuration. Also, the observation of inverted body stimuli (inversion effect) elicited an increased N190 response (Stekelenburg and de Gelder, 2004), suggesting an impairment of configuration processing of body shape when presented upside-down (Reed et al., 2003).

Another outstanding issue concerns the hemispherical lateralization of the neural substrates underlying the human body perception. Several studies showed a bilateral involvement of OTC in body processing (Cross et al., 2010; Peelen and Downing, 2005), while other authors suggested a greater specialization of the right hemisphere (Aleong and Paus, 2010; Engell et al., 2014; Vocks et al., 2010a). Aleong and Paus (2010) found a greater activity (fMRI) in the right (than left) EBA and FBA during body observation in female (but not male) participants, along with modulation of these right regions due to body size changes. Also, the right EBA was sensitive to the perspective of the observer, showing an increased response to egocentric than an allocentric point of view (Chan et al., 2004).

Finally, a debate has been opened regarding the contribution of the OTC regions in action processing. As part of the ventral stream, the OCT was classically considered related to low-level features processing (Amoruso et al., 2011), with subsequent integration of kinematic information within a broader cortical network (i.e., AON) underpinning action understanding (Rizzolatti and Sinigaglia, 2016). However, other authors pointed out a possible role of the OTC in action preparation (Kuhn et al., 2010) and comprehension (Hafri et al., 2017; Lingnau & Petris, 2012). For instance, the engagement of the EBA was found during pointing actions in the absence of visual feedback (Astafiev et al., 2004), or when an incongruent than congruent visual feedback was provided to the observer (David et al., 2007).

Moreover, Romaiguère and colleagues (2014) showed activity in the left lateral OTC (LOTC) during both execution and observation of object-directed hand actions. A more ventral portion of this region was also sensitive to action meaning, showing enhanced activation in response to meaningless than meaningful movements performed with or without the target object. The activity of this part of the LOTC was highly correlated with that of the ACC and medial prefrontal cortex. The bimodal and more dorsal part of the LOTC was instead correlated with the activity of the primary visual regions. Similarly, a previous MVPA study showed cross-modal representation for observed and performed actions in the LOTC bilaterally and left postcentral gyrus/anterior parietal cortex (Oosterhof et al., 2010).

One last example is the MEG investigation by Tucciarelli and colleagues (2015) that suggested an earlier access to abstract action representation in the LOTC rather than visuomotor regions. The participants were shown video representing pointing and grasping actions using the left or right hand. The classifier (MVPA) was able to discriminate between the two categories of goal-directed actions (reaching vs. grasping) in two different time-windows. Significant decoding was found in an early time-window (200-600 ms) in a low alpha/theta frequency band over posterior sites, that was followed by later decoding (600-1200 ms) in high alpha/beta frequency band over precentral regions. The source reconstruction estimated the source of the early time-window in the LOTC bilaterally (left for the 8 Hz), extending into the right ITG and STG, and in the left SPC/IPC (for the 6 Hz). At the same time, the neural sources in the later time-windows were located in the right precentral gyrus (for the 10 Hz) and IFG (for the 18 Hz). Overall, these results indicated that occipito-temporal cortices as the subject of visual, motor and semantic information confluence related to the observed action (Lingnau & Downing, 2015). Further evidence showed a strong coupling between the upper-limb shape and dynamic motion features in action representation reflected by the activity of the OTC (Orlov et al., 2014). A modulation of the EBA activity was also found during action observation (Cross et al., 2006; Orlandi et al., 2017) and outcome prediction (Abreu et al., 2012) as a function of increased visuomotor expertise. This was likely the results of a refined capability to encode bodily kinematic parameters as a result of acquired experience with the motor repertoire.

In summary, the neural representation of human action consists of hierarchically and functionally organized processes distributed over interconnected cortical areas (Action observation Network, AON). Each region is preferentially engaged in the processing of different aspects of goal-oriented behavior (i.e., kinematics, goal-object, outcome). Overlapping patterns of activity in these cortical regions also allow higher-level and more abstract representation of the action. The AON encompasses fronto-parietal and occipito-temporal (OTC) areas that are partially active also during action execution and imagination. Especially, the extrastriate and fusiform body areas within the OTC have a specific role in body processing but also action representation. From an electrophysiological perspective, the activity of this network results in increased desynchronization (ERD) of the mu frequency band (8-12 Hz) of the EEG recorded over the sensorimotor regions of the scalp. During mental simulation, the imagery ability and perceived vividness of the image affect the recruitment of fronto-parietal regions. More generally, visuomotor expertise (motor knowledge) has a strong impact in modulating the AON engagement due to enhanced resonance processes with the observed or imagined action.

1.2. Neuroscience of dance

Over the last decades, a growing number of neuroscientists has been focused on dance as a framework to approach the study of human brain and relative cognitive processes (Bläsing et al., 2012; Brown et al., 2008; Sevdalis and Keller, 2011). One of the potential explanations for this attention could be sought in the fact that dance is a bodily and motor discipline that integrates sports-like athletic abilities with expressive aspects of art. Specific attention can be placed in the physical aspects of dance and motor skills acquisition. In this regard, there are several techniques and different dance styles, each with a specific set of rules and principles. All the dancers trained in one of these repertoires of movement share the same theoretical and practical knowledge of it. This can be useful when a comparison between participants with a different level of expertise is required (Amoruso et al., 2014) or a match between kinematically similar movements from different techniques is necessary (Calvo-Merino et al., 2004). Moreover, the range of technical gestures is wider rather than in other sports (e.g., shoots in basketball or football). It is also possible to create novel moves (also referred to as choreographic languages or “quality of movement”) without bending motion principles (Cross et al., 2006; Orlandi et al., 2017), especially in modern and contemporary dance. Actions varying in complexity and body parts involved in the movement can be selected, considering a single step or entire sequences of steps (Orgs et al., 2013). Finally, dance can be performed and perceived at both individual and group level, becoming relevant for studies focused on joint actions and synchronicity (Himberg et al., 2018; Vicary et al., 2017). On the other side, the choreographic process can be summarized in the idea of codifying concepts and thoughts (whether they are concrete, abstract or emotionally connoted) through movement sequences, that, once perceived by the observer, can be decoded allowing the message transfer (Orgs et al., 2016). More precisely, the understanding of the semantic content is based on several aspects, including previous expertise, the knowledge of artistic patterns of the artist, the personality of the audience, and art context (e.g., music, scenography, costumes). Thus, dance appears to be a privileged framework to study the relationship between nonverbal communication, affective body language and body kinematic information (Christensen et al., 2016). In the following subparagraphs, a particular emphasis on the role of expertise in modulating the AON during action observation and imitation will be placed. Initially, studies involving professional athletes (Smith et al., 2016; Tomeo et al., 2012) and musicians (Proverbio et al., 2017) will be discussed, to further conclude the chapter with a specific focus on dance investigations.

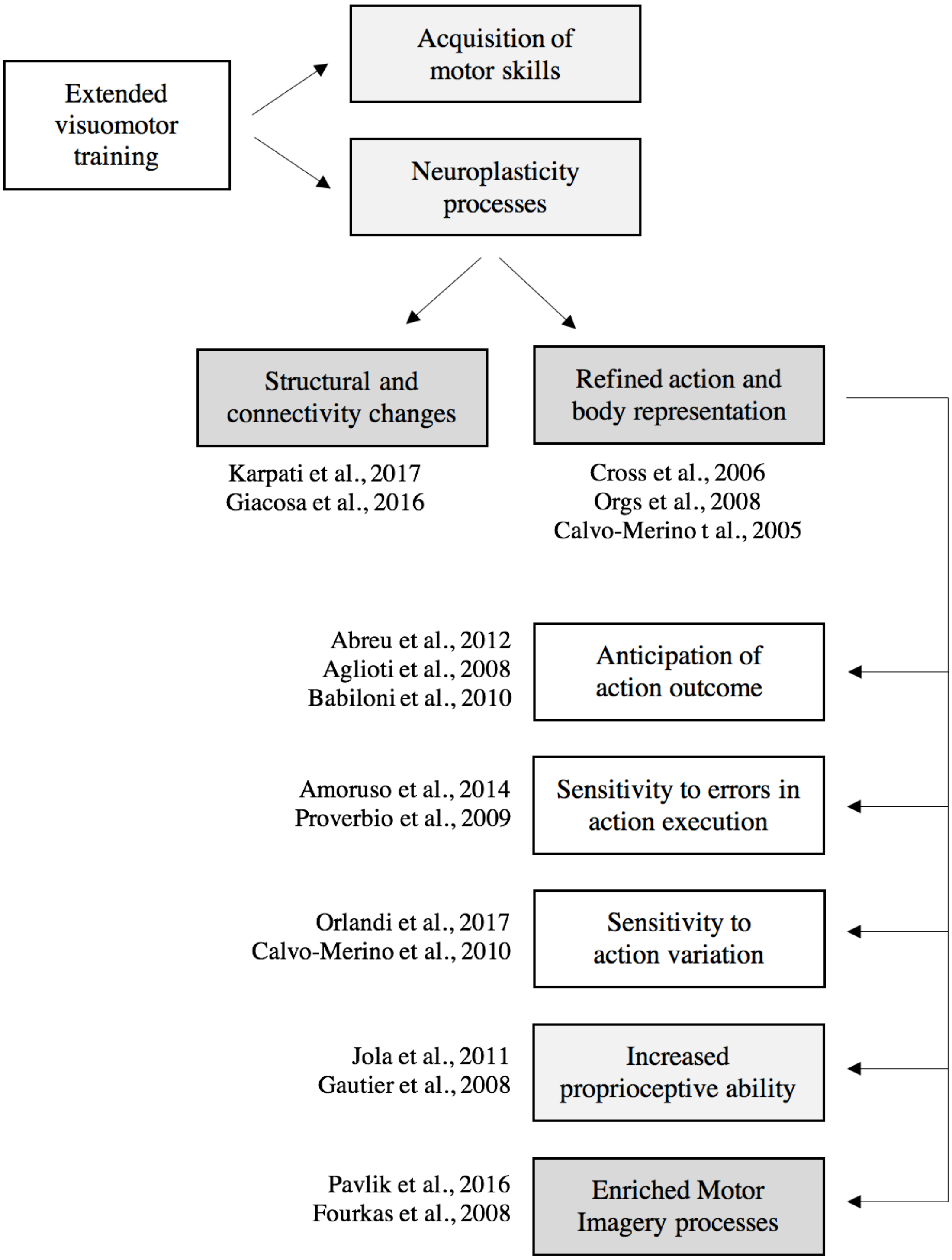


Figure 1.5. Schematic effects of visuomotor training on cognitive functions. The figure illustrates a list of cognitive functions modulated as a function of acquired visuomotor expertise. The relative author contributions are also reported.

1.2.1. Expertise-related modulation of the AON

Increasing attention has been given to the expertise framework to investigate the neural correlates of action representation (see Figure 1.5). Comparisons between experts in different areas and non-experts have pointed out behavioral and cognitive differences as a result of visuomotor practice. The intense and extensive training is at the base of every professional career in the sports and music field. This generally leads to the acquisition of specific motor skills and proprioceptive integration capability (Gautier et al., 2008; Jola et al., 2011). At the same time, these improved abilities are generally associated with neuroplasticity processes that occur in the brain of the experts. In this regard, structural, connectivity and functional changes have been found in the brain of musicians and athletes (Giacosa et al., 2016; Herholz et al., 2012; Schlaug et al., 2009). A case in point is the investigation by Giacosa and colleagues (2016), that showed changes in white matter (WM) structure related to music and dance training, by mean of the DTI (diffusion tensor imaging) technique. In that study, expert dancers, musicians, and non-expert controls underwent different behavioral tasks (Dance Imitation, Melody Discrimination and Rhythm Synchronization) and DTI measures. The group of dancers showed increased diffusivity and reduced anisotropy in several brain structure, including the corticospinal tract, superior longitudinal fasciculus, and the corpus callosum. Contrarily, reduced diffusivity and increased proportion of primary fibers in similar regions were found in musicians. Each group outperformed in the relative expertise-specific task and showed a different correlation between WM changes and behavioral performance. This evidence was seen as an index of long-term plasticity as a function of the different multisensorial training. The authors speculated that whole-body dance training might result in increased fanning of brain connection and crossing fibers. In contrast, musical training may lead to focussed enhancements of effector-specific connections.

The different development of cortical regions and connections was likely correlated with the refined processes of the neural representation of motor acts exhibited by the professionals. For instance, multi-technical evidence has demonstrated increased capability of the experts to anticipate the outcome of an action, including fMRI (Abreu et al., 2012; Blaser et a., 2012), TMS (Aglioti et al., 2008; Makris and Urgesi, 2015) and EEG (Babiloni et al., 2010; Denis et al., 2017) studies. For instance, Abreu and colleagues (2012) presented basketball players and non-players with videos depicting correct and incorrect free shots during fMRI scanning. While they were predicting the outcome of the game actions, increased activity was found within the AON regardless of their expertise level, including IFG, vPM, IPL, and somatosensory cortices. Between-group comparison showed enhanced activity in the EBA in professional, that was likely the result of a refined capability of reading body kinematics. Moreover, activity in the IFG bilaterally and right ACC when experts wrongly judged the stimuli suggested that they might be aware of their performance. At the same time, the correct identification of the stimuli led to posterior insular cortex activity in experts and orbitofrontal activity in controls. This evidence suggested the engagement of different expertise-related decision-making mechanisms. Body awareness might have played a role in experts, while high-order cognition processes were required by non-experts. In a previous study by Aglioti and colleagues (2008), the authors showed that physical practice rather than visual practice was necessary for fine-tuned execution-observation matching. Professional basketball players, expert watchers, and control volunteers were shown videos of correct and incorrect baskets shots. They were asked to predict the outcome of the movements while a TMS pulse was delivered over the left PM cortex. Only in experts, an increased corticospinal extricability was found (larger MEPs) comparing incorrect and correct actions. Contrarily, no MEPs modulation was visible in the group of expert observers or controls.

From an electrophysiological perspective, Babiloni and colleagues (2008) showed that the outcome of the actions could be predicted by the brain activity during the execution of the action itself. In their study, the authors instructed participants in executing golf putts during EEG recording. Modulation of the power in the high alpha frequency band (10-12 Hz) was found over fronto-central sites of the scalp. Particularly, an event-related reduction (ERD) of alpha power was visible when comparing brain activity during correct/successful putts with erroneous/unsuccessful putts. A linear correlation was also shown between ERD and amount of error, quantified as the distance (cm) from the target hole. The more correct and precise was the action, the stronger the reduction of alpha power. In a further study, the same research group (Babiloni et al., 2010) showed an expertise-related modulation of this event-related desynchronization. The authors presented elite karate athletes, amateur athletes and non-athlete controls with clips representing karate performances with the instruction of judging the technical level. A greater decrease (ERD) of the power in alpha frequency band was found in non-athletes than professional athletes, being specifically located over the dorsal pathway (8–12 Hz) and sensorimotor regions (10–12 Hz). At the same time, amateur athletes showed an intermediate ERD amplitude relative to the other groups. The different results in ERD were interpreted as an index of “neural efficiency” in the brain of skilled individuals as a function of acquired expertise. Recently, Denis and colleagues (2017) showed that the anticipation ability of experts was based on sensorimotor rather than visual processes. They found ERD in high mu band rhythm (8-11 Hz) over central electrodes when expert tennis players (compared with non-players) were predicting the final direction of a ball in a tennis shot. Contrarily, no between-group difference in the alpha frequency band was found over posterior visual regions.

One of the acquired skills of experts consists in their enhanced sensitivity to errors made during action execution (Candidi et al., 2014; Proverbio et al., 2012; 2017). In this regard, Proverbio and colleagues (2012) presented basketball players and non-players with images depicting game actions (i.e., defensive actions, blocking, and shooting) that could be executed correctly or incorrectly. Evident violations in body posture or technique were visible in the latter condition. The participants were engaged in a secondary target detection task during EEG recording. The observation of the erroneous actions elicited a negative component (N400) over the anterior sites of the scalp in the group of professional players but not controls. The swLORETA source reconstruction was used to estimate the neural generator of the N400, that included the STG, FG/ITG (EBA) and IPL. This evidence suggested enhanced ability to automatically detect violations in the rules of a game as a result of intensive sports practice, thought the activity of frontoparietal, associative and body-related visual regions. In a further EEG/ERP study, the same research group (Proverbio et al., 2017) presented professional musicians and non-musician controls with video clips representing fingerings (static frame of a pair of hands) in combination with congruent or incongruent piano sounds. As in the previous investigation, the participants were instructed to press a button in response to rate target stimuli. The perception of the incongruence evoked a negative component (ERN, error-related negativity) over prefrontal sites of the scalp in experts only, especially over the right hemisphere. The anterior cingulate cortex (ACC), STG, associative auditory, visuomotor and body-related regions were identified (swLORETA) as main electromagnetic dipoles explaining the distribution of the ERN. Overall, the results indicated refined representations of combined gesture and sound due to multimodal musical training.

Also, the motor imagery processes showed a modulation as a result of increased trimmed neural representation of motor acts due to acquired expertise (Fourkas et al., 2008; Pavlik et al., 2016). In a TMS study by Fourkas and colleagues (2008), tennis players and novices were instructed to imagine themselves executing a tennis forehand, a table tennis forehand and a golf drive with the right hand. Specifically, they were asked to integrate the tools in the motor image as an extension of their limb. During the mental task, they kept the arm relaxed while a single TMS pulse was delivered over the contralateral (left) primary motor cortex (M1). Larger MEPs (motor evoked potentials) were recorded during imagery of the tennis action (compared to baseline) from the hand (FDI) and forearm muscles (EIP) of experts. This modulation was significantly different from those evoked during the imagination of the other actions. Contrarily, no difference was visible between action types in the novice participants. The results indicated task-specific tuning of hand motor excitability in expert players due to more sophisticated processes of action representation.

1.2.2. Dance expertise

As mentioned in the introduction of this subchapter, evidence from the neuroscience of dance has a prominent role in investigating the brain networks underpinning motor representation. In a classical study by Calvo-Merino and colleagues (2005), a comparison between the different group of experts was made. The authors aimed at investigating the role of expertise and action kinematics in modulating the activity of the visuomotor resonance system during the observation of complex whole-body movements. Ballet and Capoeira dancers were recruited together with non-expert controls. They were presented with videos (lasting 3 seconds) depicting ballet and Capoeira movements, matched for the use of the space, kinematics and body parts involved. During fMRI scanning the participants were instructed to rate “how tiring” they thought each movement was (on a 3-point Likert scale). Activity was found in the PM cortex and IPS bilaterally, together with the right SPL and left posterior STS. Moreover, these regions were more engaged when experts were observing their specific movement style. Contrarily, no difference between stimulus type was found in non-expert controls. This evidence suggested modulation of the visuomotor system as a function of acquired motor knowledge and not visual similarity of the stimuli. In a following investigation, the same research group (Calvo-Merino et al., 2006) differentiated the influence of visual and motor expertise during action observation. Neural activity (fMRI study) of male and female ballet dancers was compared during the observation of video depicting ballet steps belonging to male, female or gender-common technique. In this way, the authors were able to compare movements that dancers were used to training (same gender technique) with those they were used to observe (opposite gender technique). The three-way interaction of subject gender, performer gender, and stimulus type showed a specific engagement of the left PM, IPC, and the cerebellum bilaterally. This result suggested a greater engagement of the motor system during the observation of action for which motor rather than visual expertise was own.

From an electrophysiological perspective, Orgs and colleagues (2008) found an expertise-related modulation in alpha and beta frequency band during the observation of complex action. They presented professional contemporary dancers and non-dancer controls with videos depicting an actor performing technical dance gestures and daily-life movements (with the upper part of the body) during EEG recording. The participants were instructed to categorize each movement. Event-related desynchronization, namely a reduction of power in specific frequency bands (7.5 – 25 Hz) was shown in the brain of experts while watching the dance steps (compared to the baseline). This modulation was found between 1 and 2 seconds after the video onset and was seen as an index of the activity of the visuomotor system. Contrarily, no difference between the two categories was found in controls, likely due to the lack of motor knowledge of the actions.

Interestingly, the impact of expertise on the activity of the AON can be observed after only a few weeks of training, as shown by Cross and colleagues (2006)'s study. Professional dancers were trained with novel sequences of whole-body movements for five weeks. Before the beginning of the training and at the end of each week, they were invited into the lab and presented with videos depicting fragments of both trained and non-trained dance sequence, during fMRI scanning. They were instructed to observe the movements, imagine themselves reproducing them, and rate their ability to perform the task. The contrast between trained and non-trained moves elicited a response of the STS, ventral PM, IPS and rostral part of the SMA. When taking into account the reproducibility ratings, a correlation was obtained with the activity in the left IPL and ventral PM. This suggested a greater activity in visuomotor regions of experts as a result of the increasing feeling of competency. Evidence of similar plasticity effects in non-dancer participants was recently found by Kirsch and colleagues (2015). They trained the volunteers for four days with dance sequences by using three different modalities. First, they were asked to physically reproduce some movements while watching them on a screen and listening to a relative soundtrack. Second, they were instructed to observe other movements accompanied by the music, without any real execution. Third, they were asked to listen to a few soundtracks alone without movements presentation. The volunteers were scanned before and after the days of training while being presented with short videos depicting fragments of the trained and non-trained sequences. The post-training imaging showed a greater engagement of the left PM, left STG and right IPC in response to trained than non-trained moves, as a function of increased multisensory experience. The scores of accuracy in reproducing the trained movements were also positively correlated with the activity in the PM cortex. Overall, this evidence seemed to suggest that acquired expertise with dance resulted in a more detailed neural representation of action. Motor resonance processes were stronger in response to intensively rehearsed than non-rehearsed movements.

As previously shown in the case of skilled musicians and sport athletes (Panasiti et al., 2016; Proverbio et al., 2012), the more sophisticated action representation of dancers results in a refined capability of perceiving errors and variations (Amoruso et al., 2014; Orlandi., 2017). For instance, Amoruso and colleagues (2014) presented professional Tango dancers, amateur dancers and non-dancer controls with videos representing a couple of dancers performing correct and incorrect Tango steps. The participants were instructed to judge the correctness of the movement at a visual cue. The observation of the erroneous actions elicited a negative component (N400) over left and middle-parietal sites of the scalp only in the group of professional dancers. This enhanced negativity was not visible in the groups of the beginners or controls. A further slow wave (SW) component was found over the same site of the scalp, showing a similar expertise-related modulation as the N400. The SW was larger in response to correct than incorrect movements only in experts. In a further study, Orlandi and colleagues (2017) demonstrated the ability of experts to perceive small variations between nearly identical complex moves automatically. Professional contemporary dancers and non-dancer controls were presented with video pairs depicting novel whole-body dance movements during EEG recording. The second video of each pair could represent a repetition of the previous movement or a subtle, varied version of it. The volunteers were instructed to observe each stimulus and press a key when a still frame (representing a dancer in a relax starting position) was presented instead of a video. Over fronto-central sites of the scalp, a negative component (N400-effect) was elicited by the presentation of modified than identical moves only in experts, at proximately 450 ms after stimulus onset. A reduction of the amplitude of a late positive component (LP) was found over centro-parietal sites in dancers but not controls. The source reconstruction (swLORETA) of the N400-effect in experts showed engagement of the bilateral STS, IPL, PM and body-, face- and motion-related visual regions. These results suggested that acquired expertise with dance principles of movement (i.e., time, space and body dynamics) allowed the experts to automatically perceive the subtle variations in action kinematics, which were indistinguishable for non-experts. This evidence was consistent with a previous finding of Calvo-Merino and colleagues (2010). In that study, the authors presented dancers and non-dancers with pairs of point-light animations depicting stereotyped ballet steps. When the movements were presented in an upright/canonical orientation, experts (than controls) were able to discriminate better whether the action was the same or different. In response to upside-down/inverted stimuli, there was a significant decreasing only in the dancers' performance, suggesting an impact of motor expertise in configurational processing of action.

At this point, it is crucial to introduce a few examples of studies that investigated brain plasticity resulting from dance practice. Several pieces of evidence showed that extended and intense visuomotor training led to plastic modulations of brain regions and connections underlying the acquisition of specific cognitive and physical abilities. In this regard, Hüfner and colleagues (2011) showed volume reduction in the anterior parahippocampal formation and parieto-vestibular cortex in experts (compared with non-experts), along with volume increasing in the posterior parahippocampal formation, fusiform and lingual gyri. While decreased grey matter (GM) was likely the result of the suppression of destabilizing vestibular input, increased GM in visual regions suggested greater use of visual information for balance. Greater grey matter (GM) volume in the primary motor and sensory regions was also found in and ballet dancers and handball players, together with a reduction of fractional anisotropy (FA) in the corticospinal tracts (Meier et al., 2016). Specifically, these changes were found in different cortical areas on the base of specific expertise. Foot-related sensorimotor regions and connections were affected in dancers, while hand-related areas were affected in handball players. Recently, Karpati and colleagues (2017) identified a thickening of the superior temporal associative areas in dancers and musicians (compared with non-trained controls). The structural modulation of this area was also positively correlated with the performance of dance imitation, rhythm synchronization, and melody discrimination tasks, among all participants. Finally, changes in the structure of the corpus callosum (CC) were found in experts when compared with non-experts (Giacosa et al., 2016; Hänggi et al., 2010), suggesting increased interhemispheric communication capability associated with the intense practice.

The last evidence that deserves consideration was provided by Poikonen and colleagues (2018), that showed an expertise-related difference in functional cortical communication during the observation of dance actions. Dancers, musicians, and non-expert controls were presented with videos depicting sequences of movements with and without music, a moving sticky figure and music alone during EEG recording. Action observation resulted in decreased alpha (8-13 Hz) phase synchrony over fronto-central and posterior electrode sites in all participants. This effect was greater in response to multimodal stimuli (dance with music) characterized by greater acceleration (than low acceleration) and seemed not to be affected by the expertise level. At the same time, increased synchrony in the theta frequency band (4-8 Hz) over fronto-central sites of the scalp was found in the dancers (compared with the other two groups of participants) while observing dance with music sequences. These results were seen as an index of more refined cortical processes and communication in multimodal processing due to acquired dance expertise. Increased spatial awareness, capability in action timing prediction, and embodied emotions understanding might underlie this enhanced theta activity.

Chapter 2

The inversion effect modulates attentive selection for object perception (bodies vs. cubes): an ERP study

«I'm always trying to turn things upside down and see if they look any better»

Tibor Kalman

2.1. Introduction

In this first experimental chapter, we investigated the visual processing and encoding of the human body in relation to the spatial orientation in the gravitational field. We focussed on cognitive processes related to explicit recognition of the body shape. Specifically, we were interested in studying how the presentation of upside-down bodies compared with upright bodies affected selective attention allocation and stimuli categorization. The study has been conducted at the Cognitive Electrophysiology lab (ERP lab) of the University of Milano-Bicocca under the supervision of the Prof. Alice Mado Proverbio.

Several pieces of evidence have shown that the perception of a human body engages specific associative visual region in the OTC (Peelen and Downing, 2007). The OTC is part of the ventral pathway devoted to the processing and progressive integration of visual information resulting in object identification and recognition (Goodale and Milner, 1992; Ishai et al., 1999). Specifically, the EBA and FBA showed selective activation in response to real images, sticky figures and silhouettes representing whole-body or body parts (Downing et al., 2001; Peelen and Downing, 2005; Schwarzlose et al., 2005). Similarly, specific activation in the FFA and OFA was found in response to images depicting faces (Kanwisher et al., 1997; Grill-Spector et al., 2004). Converging evidence from EEG, MEG, and intracranial recording studies showed that the perception of a body elicited a negative electromagnetic component at approximately 190 ms at sensor sites corresponding to OTC (Taylor et al., 2010; Thierry et al., 2006). The neural generator of this component (N190) have been located in the middle temporal gyrus (EBA) bilaterally, but with the dominance of the right hemisphere (Engell et al., 2014; Ishizu et al., 2010; Pourtois et al., 2007). Moreover, conflicting evidence has been found in favour of both configurational (Brandman et al., 2014) and local (Orlov et al., 2010; Taylor et al., 2007) body processing in the EBA. In this regard, relevant results have been provided by studies involving the presentation of upside-down stimuli.

Reed and collages (2003) have shown that when the participates are instructed to discriminate between two body postures, the inversion of the stimuli resulted in decreased discrimination ability. This effect was referred to as the body inversion effect (BIE) and manifested in both reduced accuracy and slower reaction times (RT) to inverted than upright stimuli. The BIE was absent for impossible body positions violating biomechanical constraints of the human body (Reed et al., 2003), isolated body parts (Reed et al., 2006) or disruption of first-order spatial relations, such as body parts rearranged or randomly presented (Tao et al., 2014). The BIE was also found in response to dyads of facing bodies but not of non-facing bodies or objects (Papeo et al., 2017). Moreover, Stekelenburg and de Gelder (2004) showed that upside-down bodies elicited later and larger N1 (N190) component over occipito-temporal sites when compared with the same upright bodies. While no N1 modulation was found for inverted objects, further ERP evidence corroborated the sensitivity of the N1 to the BIE (Minnebusch et al., 2008; Tao et al., 2014). For instance, a quadratic trend was shown between a gradually rotated body (from 0° to 360°) and both behavioral response and N1 amplitude (Minnebush et al., 2010). These results resembled those found for face inversion effect (i.e., modulation of N170) and suggested disruption of configurational processing for inverted bodily stimuli (Rossion et al., 2000).

At the same time, other authors showed that the BIE was strongly reduced or absent in response to a headless body and when the head position cannot be used for posture discrimination (Munnebusch et al., 2008; Yovel et al., 2010). This effect was not visible for bodies missing other parts (i.e., limbs). Thus, these results were interpreted as an index of BIE depending on the disruption of configurational processing of face rather than body. This idea was also corroborated by an fMRI study that showed a pattern of adaptation for BIE of headless and faceless bodies in face-selective (FFA and OFA) but not body-selective (EBA and FBA) regions (Brandman and Yovel, 2010). However, Susilo and colleagues (2013) investigate the inversion effect for body and face in patients suffering from acquired prosopagnosia (manifested as difficulty in face recognition). Whether reduced accuracy and slower RT was found in response to faces in patients when compared with controls, no group difference was shown in response to headless and faceless bodies. The face recognition deficit did not affect configurational body processing and the relative BIE-related impairment. Furthermore, Robbins and Coltheart (2012) showed that when the participants had to identify a person whose images was created mixing the body and face of two different individuals, they relied more on the face than body information when the stimulus was upright presented. However, this advantage for the face was not present during the inverted presentation. Also, BIE was found for face, body, and headless body stimuli, consistently with the idea of configurational processes underlying the processing of both bodies and faces. Thus, they suggested that the focus on nonbody aspects (i.e., clothes) or task-related (i.e., identity vs. pose recognition) reasons may account for the lack of BIE for headless bodies found in previous studies. Finally, Arizpe and colleagues (2017) showed the independent contribution of the configurational processing (upright vs. inverted) and eye gaze (towards head, torso, and pelvis) to the BIE. Reduced discrimination performance was found for whole body stimuli when the participants were instructed to keep their eyes fixed on a lower (pelvis) than higher body location (head/torso). At the same time, no difference was visible for headless bodies stimuli, and more importantly, these effects were independent of the orientation.

The majority of EEG studies presented so far indexed the BIE with the modulation of the N1 amplitude (and latency). At present, there is a lack of evidence on neural substrates and cognitive processes underlying the BIE. Contrarily, a few studies investigated the role of visual regions during the inversion effect for faces (Haxby et al., 1999) showing reduced activity in the FFA for inverted than upright faces (Kanwisher et al., 1998; Yovel et al., 2005). In addition to N1 modulation, a few studies focussed on categorization processes (Zhang et al., 2012) and attention allocation towards face stimuli (Eimer, 2000). Thus, the present study aimed at extending previous ERP findings on inversion effect for bodies, particularly focusing on the relationship between selective attention, stimuli categorization and inverted body perception.

In literature, a number of different tasks have been used in BIE studies, including same-different judgment of postures (Reed et al., 2003), orientation discrimination (Stekelenburg and de Gelder, 2004) and identity detection (Robbins and colleagues, 2012). Here, we focussed on the recognition of the body shape per se, presenting the bodies in both upright and inverted orientation. We created stimuli using 3D graphics representing the shape of the human body in different poses. Precisely, a mannequin template was used, so that only the 3D shape was visible, but not details like face, hair, fingers of clothes. Thus, we avoided any artefact due to the manipulation of the body stimulus (i.e., face blurring or head removal). Furthermore, all BIE studies in which real objects (i.e., house, chair, bottle, shoes) were used as control condition for the body, no effect of inversion was found in both behavioral and electrophysiological results (Stekelenburg and de Gelder, 2004; Reed et al., 2006; Zhou et al., 2010). Also, visual features between the different categories of stimuli were somewhat different (i.e., level of details, space distribution). Consequently, we decided to compare our bodies with cubes to keep them visually alike as possible. We used modular structures made of cubes similar to Shepard and Metzler's objects (1971) used is their classic mental rotation tasks. So, for each body pose, we resembled the distribution of the body parts in the visual space using the cubes and ensured the same amount of non-empty pixels (percentage) between the two categories of stimuli. The participants were instructed to press a button in response to a specific target stimulus (body or cubes) regardless of its orientation. The target category was specified by the experimenter at the beginning of each run.

From the electrophysiological perspective, an extensive literature has linked visual attention allocation and stimuli categorization with the modulation of several ERP components, including the N2 over frontal and posterior sites of the scalp and the partial P300 (Patel and Azzam, 2005). Specifically, the frontal N2 showed to be larger in non-target/no-go condition (than target/go condition) indexing motor inhibition and conflict monitoring, being also sensitive to stimulus categorization (Folstein and Van Patten, 2008; Folstein et al., 2008). Over posterior and parietal regions, an inverse pattern was shown for the N2 and P300 responses respectively, with enhanced components elicited by target than non-target stimulus. The difference wave obtained by subtracting the N2 evoked by target-minus-non-target was usually referred to as selection negativity, as used as an index of object-centered visual attention (Molholm et al., 2007; Zani and Proverbio, 2003). In those studies, the SN was generally followed by a parietal P300, reflecting updating the mental representation of stimulus context, item categorization, and visual awareness (Picton et al., 1992; Polich, 2007).

By this brief overview, we firstly expected to replicate previous behavioral findings showing increased accuracy and faster RT for upright than inverted bodies. Secondarily, we hypostatized modulation of N2, SN and P300 components as a function of the stimulus category and orientation (Patel and Azzam, 2005). Precisely, we speculated that bodies would elicit increased N2 amplitude over frontal sites than cubes stimuli, as an index of advantage in body stimuli processing (Batty and Taylor, 2002; Zani et al., 2015). This would be consistent with the existence of specific body-related visual regions (Peelen and Downing, 2005; Striem-Amit et al., 2014; Rui et al., 2016). Moreover, we expected larger SN and P300 in response to inverted than upright bodies, as a result of the increased allocation of visual attention (Molholm et al., 2007; Proverbio et al., 2004) and categorization processes (Zhang et al., 2012; Mudar et al., 2015) respectively. Contrarily, no modulation of these two components was assumed in response to upright and inverted cubes, given the lack of natural orientation for this category of stimuli (Stekelenburg and de Gelder, 2004; Reed et al., 2006). Overall, we hypothesized an orientation-dependent perception of the body shape. Finally, the source reconstruction (swLORETA) of the SN should point out enhanced engagement of cortical regions required to recognize body presented in unnatural than natural orientation. This network would include prefrontal, temporal, and limbic areas related to working memory, attention allocation, and stimuli representation (Benoit et al., 2011; Haxby et al., 1999; Patterson and Schmidt, 2003).

2.2. Methods

2.2.1. Participants

Thirty-two right-handed students of the University of Milano-Bicocca participated in the present investigation (19 females and 13 males). They were between 19 and 43 years of age (mean age: 25.19 years, SD = 4.75) and had normal or correct-to-normal vision. The volunteers reported no history neuropsychology disorder or drug abuse. Their right-handedness was assessed using the Italian version of the Edinburgh Handedness Inventory (mean index score: 0.79, SD = 0.17). The study was approved by the ethical committee of the University of Milano-Bicocca, and all participants signed the informed consent before initiating the experiment.

2.2.2. Stimuli

160 different 3D graphics images were created using Blender 2.79 software and employed as stimulus material. 80 of them depicted a human body while the other 80 represented cubes. 3D stimuli of the two categories were designed to be as similar as possible from a visual perspective, allowing a direct comparison between them. A combination of geometrical modular structures was used for this purpose. The body category consisted of a mannequin template without details as the face, hair, hands/feet or clothes, composed of cylinders of different dimensions. The cubes category was based on the classical stimuli by Shepard and Metzler (1971) and consisted of structures of cubes. Moreover, a light wood-like texture was applied to all stimuli, which were presented on a white background. Specifically, 16 different models were generated for the body category by rotating one or two modules of the mannequin by 90° and/or 180° (i.e., left arm stretched forward and right arm to the side). 16 models of cubes created to visually match the previous category and ensure a similar distribution in the visual quadrants between bodies and cubes. Each of the 32 models was then rotated along the vertical/longitudinal axis (z-axis), resulting in 5 different points of view (-40°, -20°, 0°, +20°, +40°). Thus, we obtained 80 different pictures of bodies and cubes amounting to 160 stimuli. The last step consisted of the 180° rotation of all the images along the sagittal axis (x-axis) to obtain upside-down (down) and upright (up) orientations (see Figure 2.1). The final pool of stimuli included 320 items (2 categories X 16 models X 5 z-axis rotations X 2 x-axis rotations). Their maximum size was 3.75 X 3.95 cm, subtending a visual angle of 1° 53’ X 1° 59’. A computation of the percentage of the non-white pixel was

performed to assess the volume occupation of each image (Image Color Summarizer - *http://mkweb.bcgsc.ca/color-summarizer*). ANOVA showed no difference in the amount of non-empty pixels ($\approx 10.82\%$, $p = 0.68$), neither in stimulus luminance ($\approx 246.49\ cd/m^2$, $p = 0.12$), as a function of stimulus category.

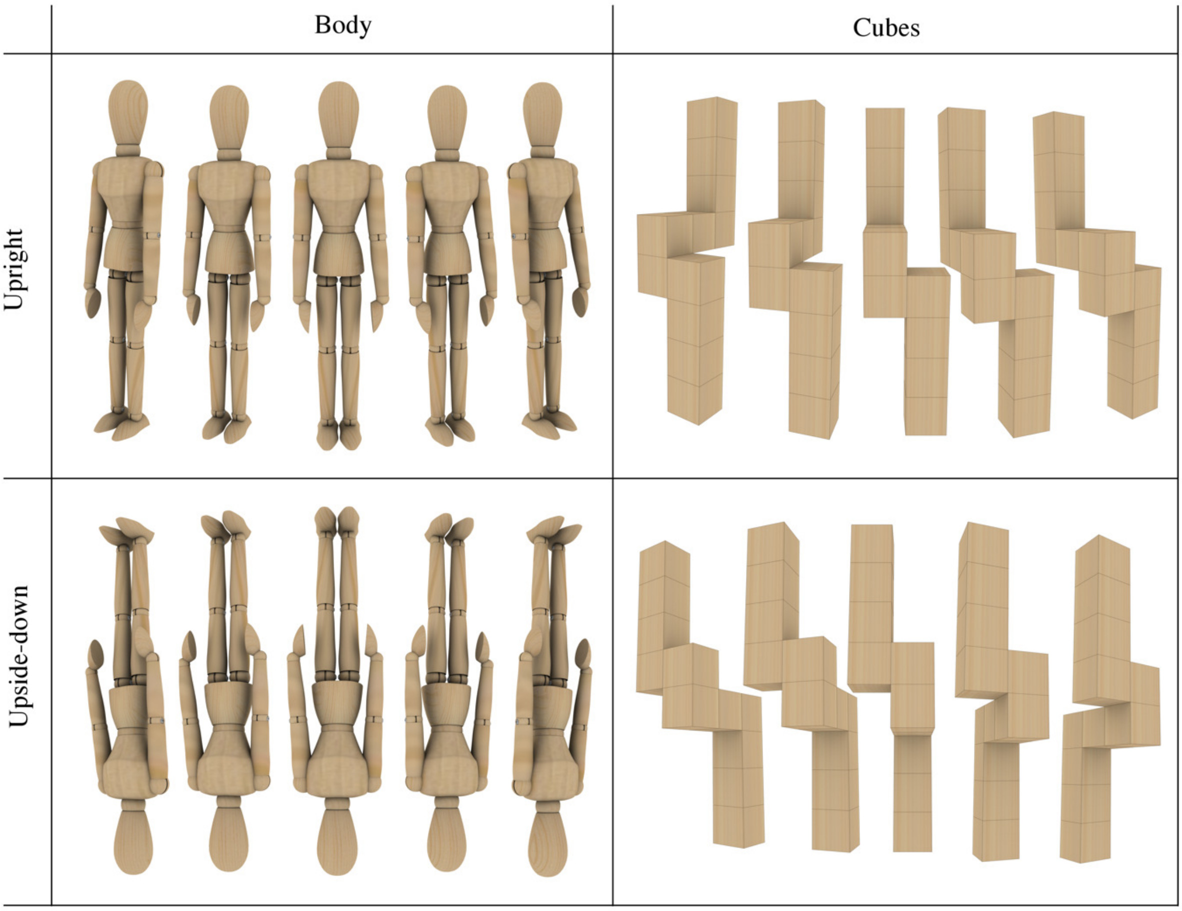


Figure 2.1. Example of stimuli used in the present investigation. The figure illustrates examples of stimuli used during the experiment. The shape of bodies and cubes were created in 3D graphics. 16 exemplars for category were designed and then rotated along the vertical axis to obtaine 5 images for each exemplar (0°, ±20°, ±40°). The stimuli were also rotated along the sagittal axis to obtain both upright and upside-down stimuli. A total of different 320 stimuli were created.

2.2.3. Task and Procedure

After signing the informed consent and compiling the right-handedness questionnaire, participants were prepared for EEG recording by placing the EEG-cap on their head. Then, they were invited to seat in an electrically and acoustically shielded cabin, where they faced a high-resolution VGA computer screen at a distance of 114 cm. For the entire duration of the experiment, a fixation dot was placed at the center of the monitor. Volunteers were instructed to look at it during each recording session to minimize blinks and movements of the eyes, head, and body. Eevoke v2.2 software (ANT software, Enschede, The Netherlands) was used for the stimuli presentation. Each image was shown at the center of the screen for 500 ms and was followed by the next one after 900 ± 100 ms (inter-stimulus interval, ISI). During the ISI a white background was displayed (see Figure 2.2). Twelve different short runs were created and presented in a pseudorandomized order to the participants. Each run included pseudorandomized body and cubes, counterbalanced for category and orientation (up, down). The 320 stimuli were repeated twice, but the same image was presented only once in every run. Volunteers were presented with a standardized written version of the experimental instruction. They were instructed to recognize one of the two categories of stimuli (target) regardless of the orientation of the item, by pressing a response button with the index finger. For each run, the experimenter verbally informed the participants on the specific target. The hands were alternately used between runs, and the order was counterbalanced between volunteers. Before the actual experiment, participants were presented with two additional training runs (consisting of stimuli not used in the real investigation) to familiarize with the task. They were blinded by the aim of the study and stimuli features.

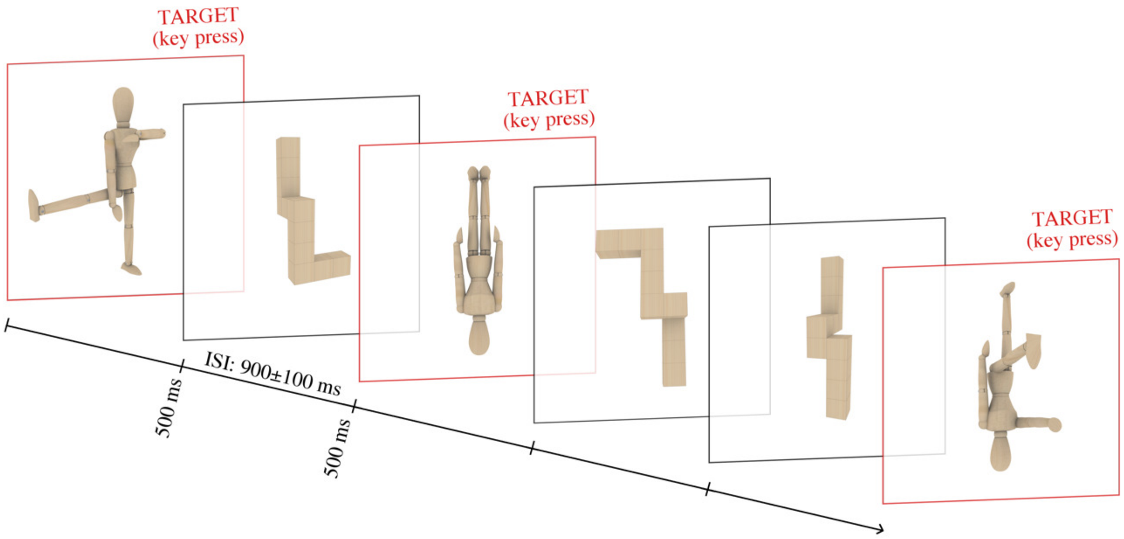


Figure 2.2. Timescale of the experimental design. Each experimental trial consisted in a counterbalanced presentation of pictures depicting a body and cubes in both upright and upside-down orientation. The stimuli were displayed for 500 ms with an ISI (inter-stimulus interval) of 900±100 ms. The participants were instructed to press a button in response to a target category, verbally indicated by the experimenter as the beginning of each run.

2.2.4. EEG recording

EEGs were continuously recorded from 128 scalp sites located according to the 10–5 International System (Oostenveld and Praamstra, 2001) at a sampling rate of 512 Hz, using EEProbe v2.2 (ANT software, Enschede, The Netherlands). Horizontal and vertical eye movements were also recorded. Averaged mastoid served as the reference lead. The EEGs and electrooculograms were amplified and filtered with a half-amplitude band-pass of 0.16–70 Hz (notch of 50 Hz). Electrode impedance was kept below 5 kΩ. Computerized artifact rejection was performed before averaging to discard epochs in which eye movements, blinks, excessive muscle potentials, or amplifier blocking occurred. The artifact rejection criterion was based on peak-to-peak amplitudes exceeding 50 μV. Moreover, trials wrongly recognized as a target (errors) or non-target (omissions) were also manually rejected. EEG epochs were synchronized with the onset of the image. ERPs were averaged off-line from −100 ms before to 1000 ms after stimulus onset and filtered with a band-pass of 0.16–30 Hz. ERP components were identified and measured with reference to the average baseline voltage calculated over the 100 ms before the stimulus onset at sites and latency when maximum amplitude was reached (Picton et al., 2000) and based on previous literature. ERP averages were computed as a function of attention, category, orientation, electrodes, and hemisphere factors.

2.2.5. Data analysis

Behavioral data

Accuracy (percentage of hit), reaction times (RTs) and errors (percentage of wrong response to non-target) in response to target images were also recorded and measured. Repeated measures ANOVAs with three within-groups factors (category: body, cubes; orientation: up, down; hand: left, right) were performed on the mean RTs, and percentages of hit and error.

Electrophysiological data

Three event-related components were measured and analyzed: an anterior N2 component, a posterior Selection Negativity, and a parietal P300. The peak latency and amplitude voltage of the anterior N2 component was measured at AFF1, AFF2, F1, and F2 electrode sites during the 220-280 ms time window. The mean area voltage of the Selection Negativity (SN) component was measured at PO7, PO8, PPO9h, and PPO10h electrode sites, the time window of 30 ms was slightly shifted to include maximum peak based on visual inspection of single-subject ERPs (approximately between 235 and 280 ms). The mean area voltage of the parietal P300 component was measured at CPz, Pz, and POz electrode sites during the 350-450 m time window (see Figure 2.3). The N2 and SN data were subjected to multifactorial repeated measures ANOVA with five within-groups factors, including: attention (non-target, target), category (body, cubes), orientation (up, down), hemisphere (left, right), and electrode (2 levels depending on the ERP component of interest) factors. The P300 data were subjected to multifactorial repeated measures ANOVA with four within-groups factors, including attention (non-target, target), category (body, cubes), orientation (up, down), and electrode (CPz, Pz, POz) factors. Multiple comparisons were computed using Tukey's post-hoc tests, and all the ANOVAs were performed using Statistica software (version 10) by StatSoft.

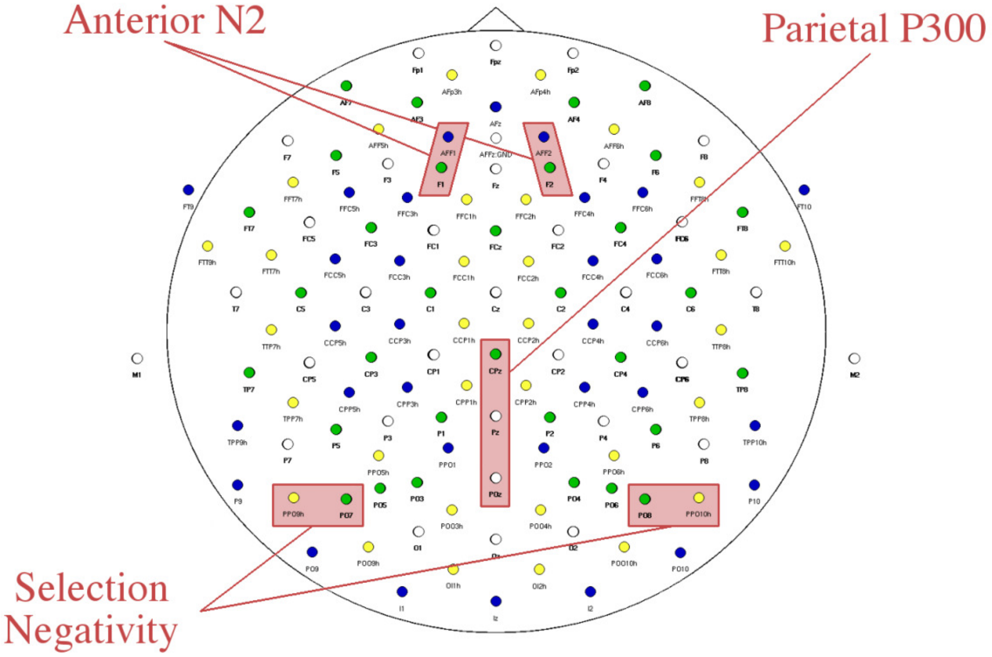


Figure 2.3. Schematic representation of the 128 electrode sites. The figure illustrates the position of the 128 electrodes on the scalp and those selected for the measurement of the three ERP components of interest.

Standardized weighted low-resolution electromagnetic tomography (swLORETA) was applied to the difference waves obtained by subtracting the ERPs for the non-target stimuli from those elicited by target stimuli in the SN time-window (body up: 235-265 ms; body down: 255-285 ms; cubes: 250-280 ms) in both upright (up) and upside-down (down) conditions. 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), regarding orientation and strength, between neighboring neuronal populations (represented by adjacent voxels). In this study, an improved version of standardized weighted low-resolution brain electromagnetic tomography (sLORETA) was used. This version incorporates a singular value decomposition-based lead field weighting: swLORETA (Palmero-Soler et al., 2007). Source space properties included the following: grid spacing (the distance between two calculation points) = 5 points and the estimated signal-to-noise ratio (SNR, which defines the regularization; a higher value for SNR means less regularization and less blurred results) was 3. LORETA 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.

2.3. Results

2.3.1. Behavioral results

Accuracy rate (hits)

Repeated measure ANOVA performed on the accuracy rate (percentage transformed in arcsin) showed a significant effect of stimulus category [$F(1, 31) = 6.69$, $p = 0.015$]. Although the percentages of accuracy were very high for both categories, the human body (99.7%) was easier to recognize related to the cubes (99.2%).

Reaction Times (RTs)

Repeated measure ANOVA performed on the RTs to target stimuli showed faster responses to body (416 ms, SE = 6.12) than cubes (435, SE = 6.59), as suggested by the significance of the category factor [$F(1, 31) = 30.56$, $p < 0.0001$].

The further category X orientation interaction was also statistically significant [$F(1, 31) = 21.89$, $p < 0.0001$]. Post-hoc tests showed that participants press the button faster in response to the body (than cubes) in both upright (up body: 412 ms, SE = 6.13; up cubes: 437 ms, SE = 7.03; $p = 0.0002$) and upside-down orientation (down body: 421 ms, SE = 6.27; down cubes: 433 ms, SE = 6.32; $p = 0.0002$). Furthermore, while RTs were slower for down

(421 ms, SE = 6.27) than up (412 ms, SE = 6.13) body (*p* = 0.0007), no difference in RTs was found for cubes as a function of orientation (see Figure 2.4).

Lastly, the category X hand interaction [F(1, 31) = 5.56, *p* = 0.025] and relative post-hoc comparisons showed faster RTs using the right (412 ms, SE = 6.55) than left (412 ms, SE = 6.25) hand in response to body (*p* = 0.045), but not cubes (*p* = 0.94).

Error rate

Repeated measure ANOVA performed on the error rate (percentage transformed in arcsin) did not show any significant difference. Nevertheless, the category factor showed a quite strong trend [F(1, 31) = 3.62, *p* = 0.066]. The volunteers wrongly indicated non-target stimuli as a target more frequently for cubes (0.7%) than bodies (0.4%).

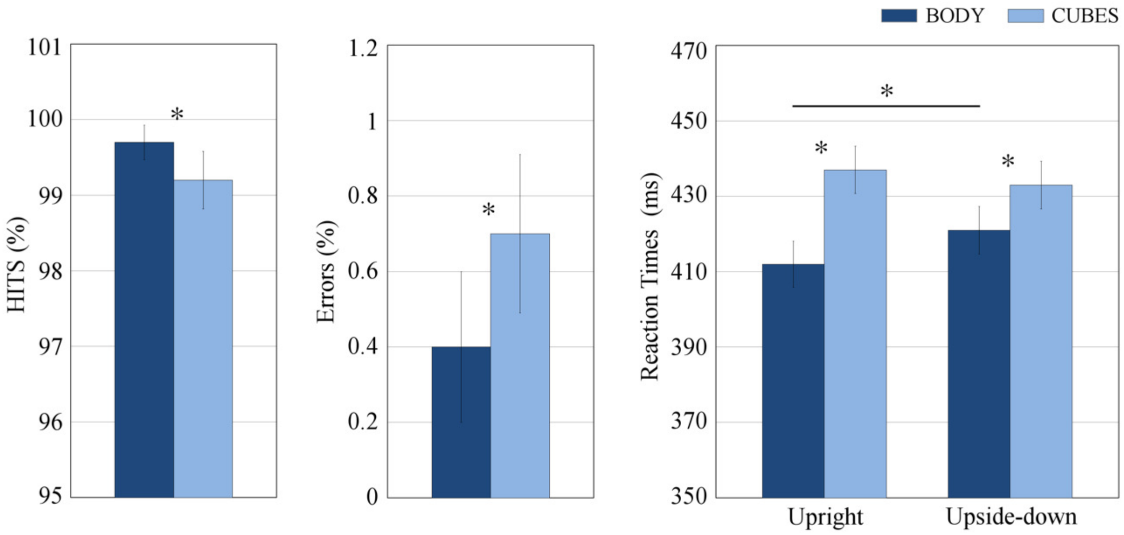


Figure 2.4. Behavioral results. The histograms display the percentages of correct responses (on the left), the percentage of errors (in the middle), and the reaction times (on the right) expressed in milliseconds (ms) to target stimuli.

2.3.2. *Electrophysiological results*

Selection Negativity, SN (250-300 ms)

The repeated measures ANOVA performed on the amplitude values (μV) of the SN showed a more negative component in response to target (4.19 μV, SE = 0.47) than non-target (5.22

μV, SE = 0.44) stimuli, as suggested by the significant attention factor [F(1, 31) = 45.800, $p <$ 0.0001].

The SN was also larger over PPO9h-PPO10h (4.45 μV, SE = 0.45) than PO7-PO8 (4.97 μV, SE = 0.45) electrode sites [F(1, 31) = 21.228, $p <$ 0.0001].

A more negative SN was found over the left (3.59 μV, SE = 0.41) than right (5.83 μV, SE = 0.57) hemisphere [F(1, 31) = 28.261, $p <$ 0.0001].

The significant hemisphere X attention interaction [F(1, 31) = 32.336, $p <$ 0.0001] and relative post-hoc tests indicated that the SN component was larger over the left (than right) hemisphere in response to bot target (left: 2.81 μV, SE = 0.42; right: 5.58 μV, SE = 0.59; p = 0.0002) and non-target (left: 4.37 μV, SE = 0.42; right: 6.08 μV, SE = 0.55; p = 0.0002) stimuli.

The hemisphere X orientation interaction [F(1, 31) = 5.984, p = 0.02] suggested a larger negativity over the left (than right) hemisphere elicited by both up (left: 3.55 μV, SE = 0.42; right: 5.63 μV, SE = 0.54; p = 0.0002) and down (left: 3.36 μV, SE = 0.41; right: 6.03 μV, SE = 0.61; p = 0.0002) orientations. Moreover, while no difference between up and down stimuli was found over the left hemisphere (p = 1.00), the SN was larger for up than down non-target stimuli over the right hemisphere (p = 0.01).

Finally, the triple attention X orientation X category interaction [F(1, 31) = 6.292, p = 0.018] showed a larger SN elicited by down (5.07 μV, SE = 0.41) than up (6.06 μV, SE = 0.56) non-target (vs. target) stimuli only for body (p = 0.0004), but not cubes (p = 1.00). See Figure 2.5, Figure 2.6, and Figure 2.7.

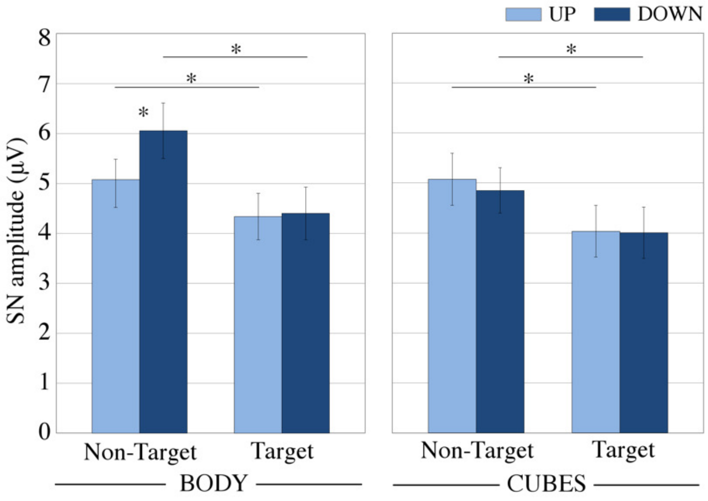


Figure 2.5. Amplitude values of the selection negativity (SN). The histogram shows the amplitude values (μV) of the SN component recorded over occipito-temporal sites as a function of the category, attention and orientation factors. The N2 potential was more negative in response to target than non-target stimuli in both body and cubes categories. Moreover, the difference between target and non-target was larger in response to upside-down than upright bodies. No similar difference was shown for the cubes.

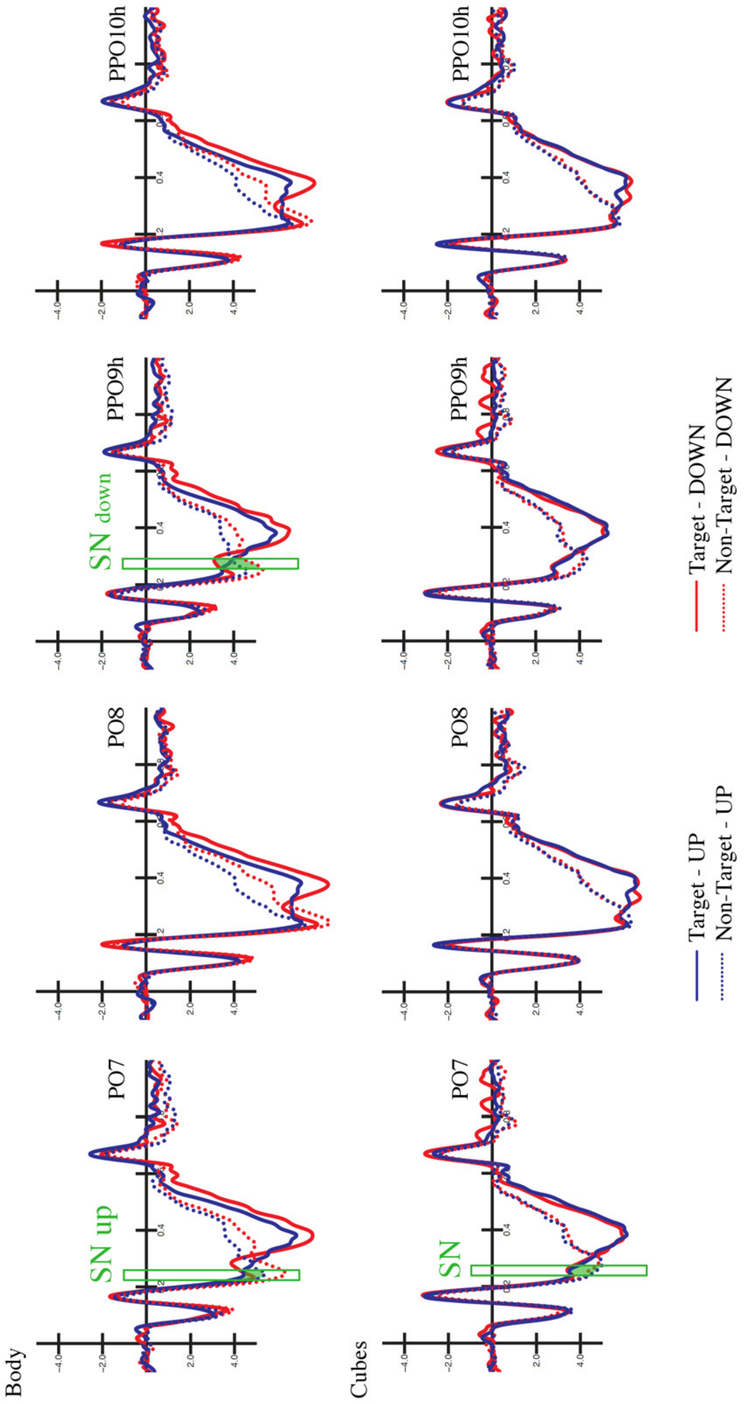


Figure 2.6. Grand average waveforms recorded at occipito-temporal sites. Grand average waveforms (ERPs) recorded over occipito-temporal sites in response to body (top panel) and cubes (lower panel). The solid lines depict ERPs evoked by target stimuli, while dotted lines represent ERPs to non-target stimuli. Upright stimuli (up) are shown in blue and upside-down stimuli (down) in red.

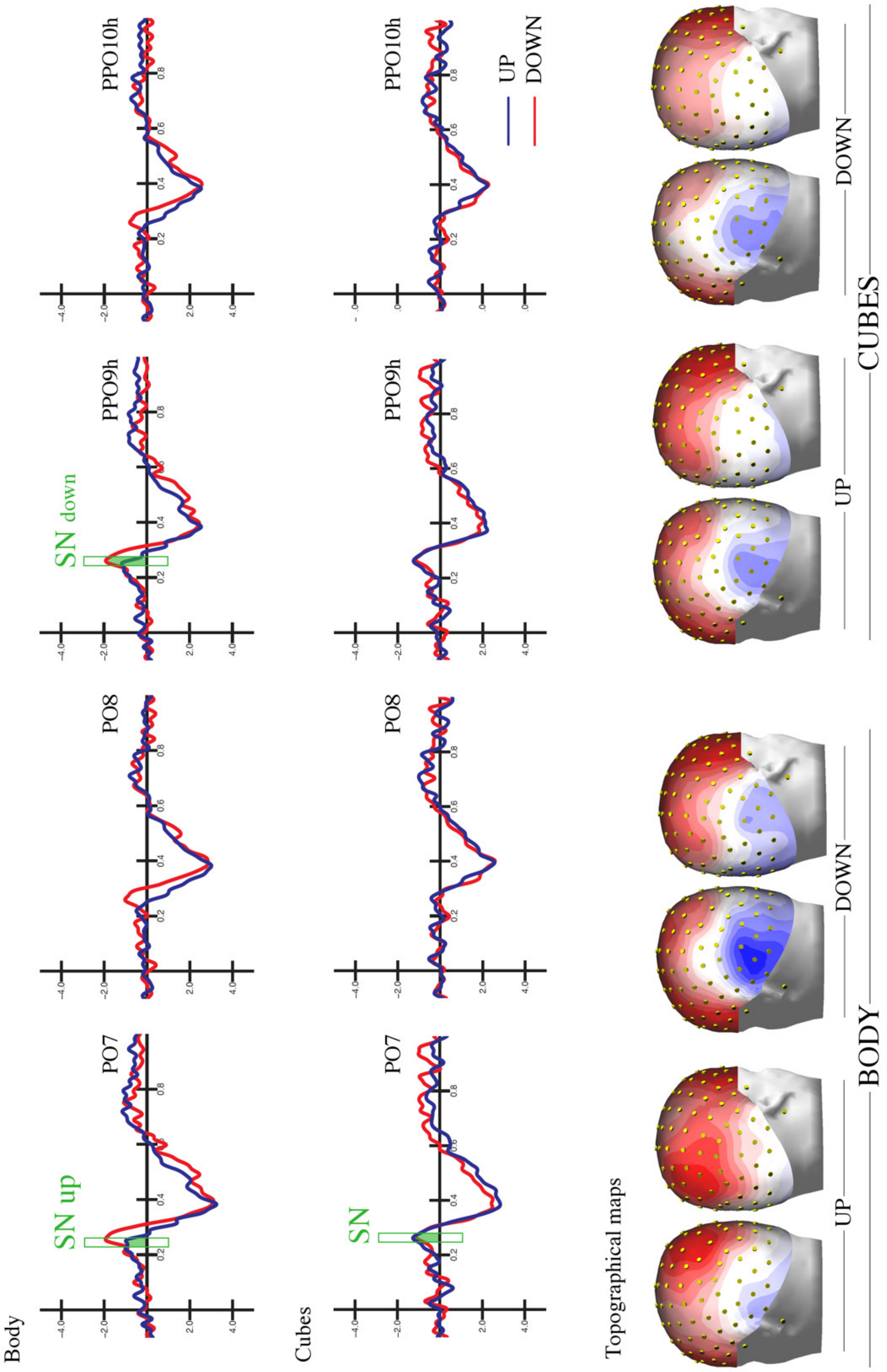


Figure 2.7. Grand averages waveforms (*difference wave*) recorded at occipito-temporal sites and topographic maps of voltage distribution over the scalp. Grand average waveforms (ERPs) of the *difference wave* target -*minus*- non-target recorded over occipito-temporal sites in response to body (top panel) and cubes (lower panel). The topographic maps computed over the *difference wave* in the SN time windows (adjusted for each category) shows an enhanced response elicited by the upside-down than upright body, while no difference is visible for the cubes. The positive values of voltage are shown in red and the negative values in blue.

Anterior N2 Amplitude

Repeated measure ANOVA performed on the amplitude values (μV) of the N2 component showed larger negativity to non-target (-3.83 μV, SE = 0.58) than target (-2.19 μV, SE = 0.61) stimuli, as suggested by the significance of the attention factor [F(1, 31) = 31.392, $p < 0.0001$].

The significant attention X electrode interaction [F(1, 31) = 14.144, $p = 0.0007$] and relative post-hoc tests ($p = 0.003$) indicated that the N2 elicited by non-targets was larger over prefrontal AFF1-AFF2 (-3.92 μV, SE = 0.58) than frontal F1-F2 (-3.74 μV, SE = 0.58) sites.

The component was also more negative in response to body (-3.74 μV, SE = 0.58) than cubes (-3.74 μV, SE = 0.58), as shown by the significant category factor [F(1, 31) = 22.144, $p < 0.0001$].

Finally, the category X attention interaction [F(1, 31) = 8.279, $p = 0.007$] confirmed the N2 component was larger in response to body than cubes in both non-target (body: -4.79 μV, SE = 0.61; cubes: -2.88 μV, SE = 0.60; $p = 0.0002$) and target (body: -2.66 μV, SE = 0.62; cubes: -1.72 μV, SE = 0.64; $p = 0.003$) conditions (see Figure 2.8, Figure 2.9, and Figure 2.10). Overall, the N2 elicited by non-target was larger than that elicited by target in both body ($p = 0.0002$) and cubes ($p = 0.0004$) category.

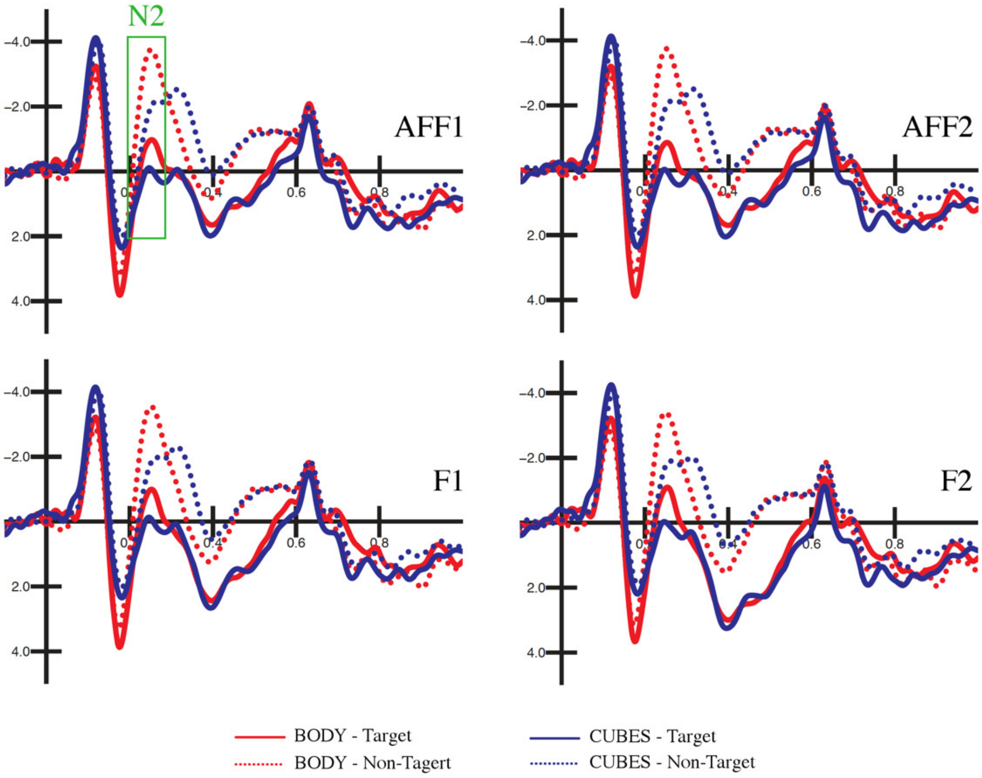


Figure 2.8. Grand average waveforms recorded at frontal sites. Grand average waveforms (ERPs) recorded over frontal sites in response to body (in red) and cubes (in blue). The solid lines depict ERPs evoked by target stimuli, while dotted lines represent ERPs to non-targets.

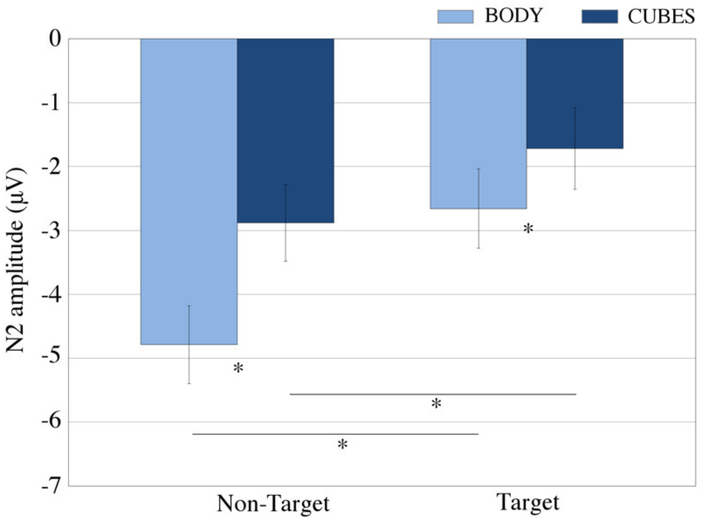


Figure 2.9. Amplitude values of the N2 component. The histogram shows the amplitude values (μV) of the N2 component recorded over frontal sites as a function of the category and attention factors. The N2 potential was larger in response to non-target than target stimuli in both body and cubes categories. Moreover, the bodies elicited a more negative response than the cubes.

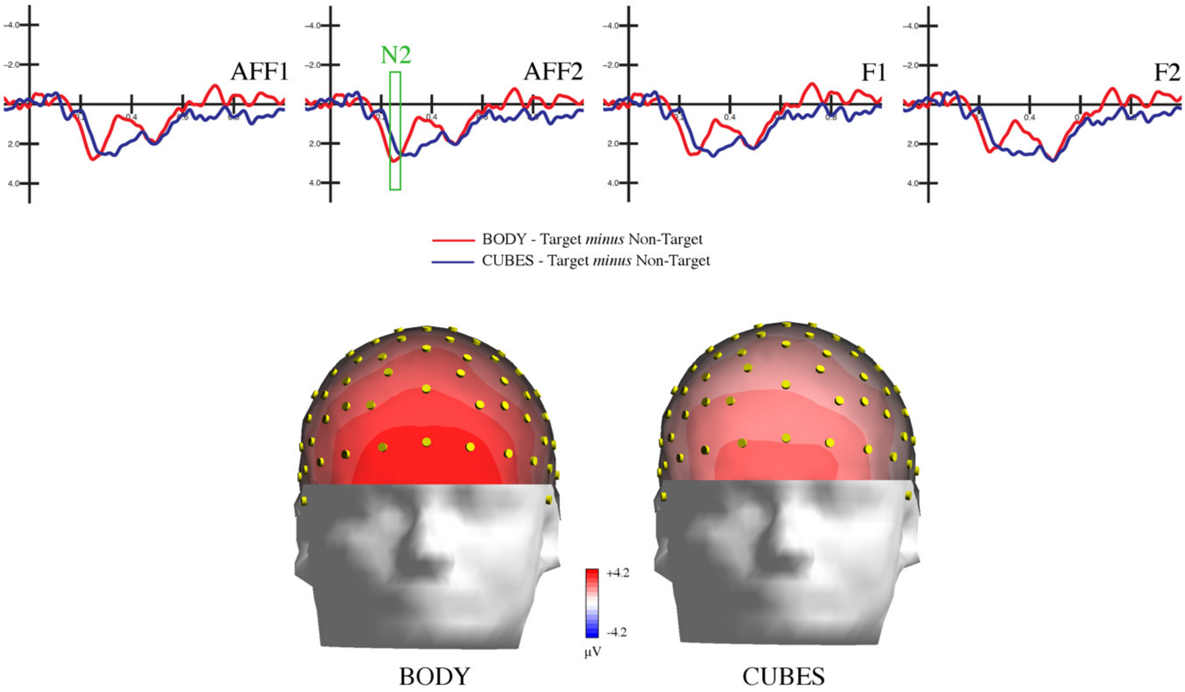


Figure 2.10. Grand averages waveforms (*difference wave*) recorded at frontal sites and topographic map of voltage distribution over the scalp. Grand average waveforms (ERPs) of the *difference wave* target -*minus*- non-target recorded over frontal sites in response to body (in red) and cubes (in blue). The topographic map computed over the *difference wave* in the N2 time window (240-260 ms) shows an enhanced response elicited by the body than cubes. The positive values of voltage are shown in red and the negative values in blue.

Anterior N2 Latency

The repeated measure ANOVA performed on the N2 latency values (ms) showed an earlier N2 elicited by body (249 ms µV, SE = 3.74) than cubes (252 ms, SE = 3.96), as suggested by the significance of the category factor [F(1, 31) = 4.509, *p* = 0.04].

The further category X attention interaction [F(1, 31) = 7.565, *p* = 0.01] showed that the faster N2 to body (than cubes) was visible only for non-target (body: 248 ms, SE = 3.43; cubes: 256 ms, SE = 3.69; *p* = 0.005) but not target (*p* = 0.99), as also confirmed by the relative post-hoc comparisons. Overall, no difference in the N2 latency elicited by the body was found as a function of the attention (*p* = 0.95). Contrarily, the N2 in response to non-target cubes (256 ms, SE = 3.69) was slower than that elicited by target (249 ms, SE = 4.885) cubes (*p* = 0.01).

The orientation factor also reached the statistical significance [F(1, 31) = 8.307, *p* = 0.007], showing a faster N2 in response to up (249 ms, SE = 3.76) than down (253 ms, SE = 3.86) stimuli.

Lastly, the significant orientation X category interaction [F(1, 31) = 6.773, *p* = 0.014] and relative post-hoc tests showed that this faster N2 for up than down stimuli was visible only for the body (up: 245 ms, SE = 3.79; down: 253 ms, SE = 3.89; *p* = 0.006), but not cubes (*p* = 1.00). See Figure 2.11 and Figure 2.12.

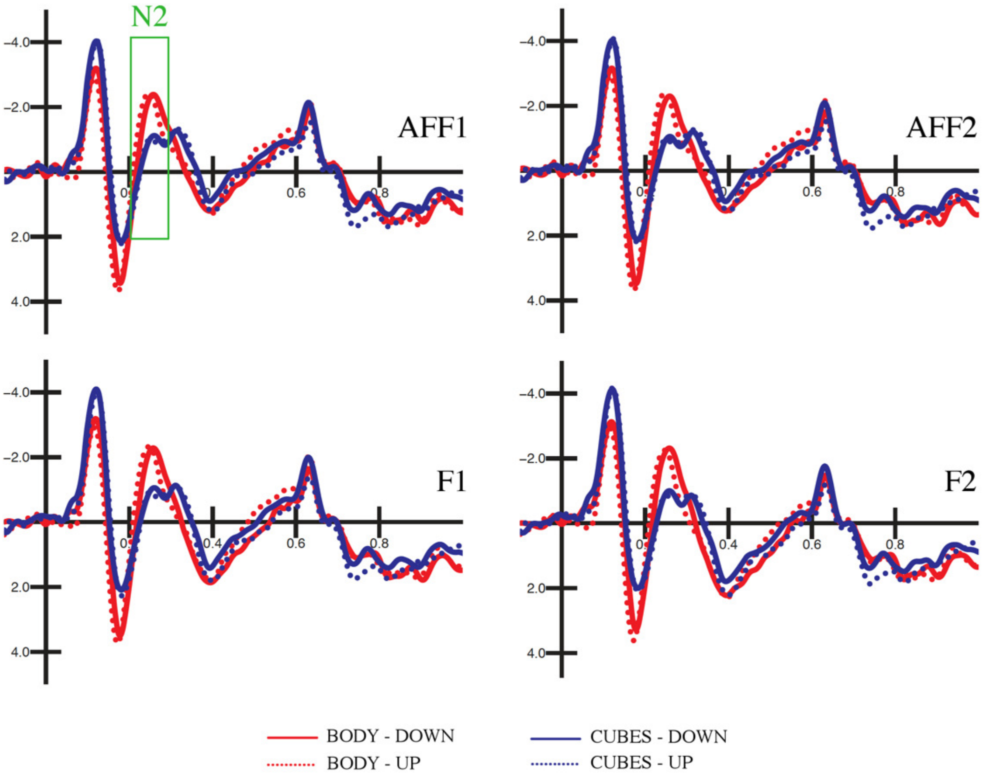


Figure 2.11. Grand average waveforms recorded at frontal sites. Grand average waveforms (ERPs) recorded over frontal sites in response to body (in red) and cubes (in blue). The solid lines depict ERPs evoked by upside-down (down) stimuli, while dotted lines represent ERPs to upright (up) stimuli.

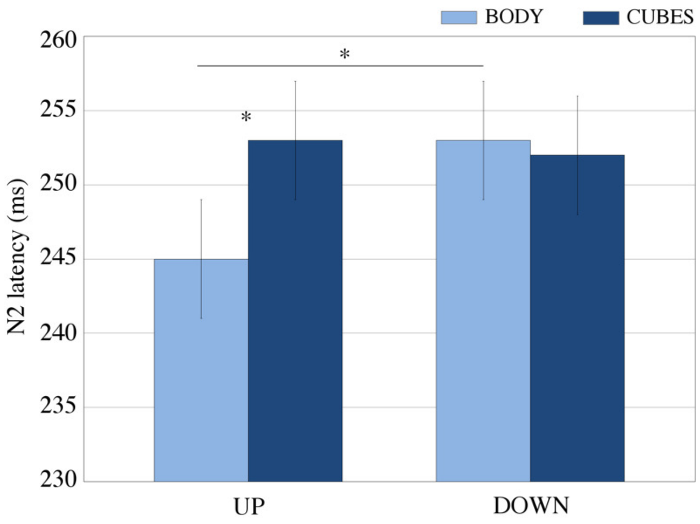


Figure 2.12. Latency values of the N2 component. The histogram shows the latency values (ms) of the N2 component recorded over frontal sites as a function of the category and orientation factors. The N2 potential was faster in response to the upright body than cubes, and to the upright body relative to the upside-down body.

Parietal P300 (350-450 ms)

The repeated measure ANOVA performed on the P300 amplitude values (µV) showed a larger component elicited by target (9.70 µV, SE = 0.77) than non-target (3.02 µV, SE = 0.49) stimuli, as suggested by the significant attention factor [F(1, 31) = 144.21, $p < 0.0001$].

A larger positivity was also found in response to down (6.63 µV, SE = 0.58) than up (6.08 µV, SE = 0.59) stimuli, as shown by the orientation factor [F(1, 31) = 20.87, $p < 0.0001$].

This difference was significant over all three electrode sites as shown by the orientation X electrode interaction [F(2, 62) = 5.582, $p = 0.006$] and the relative post-hoc tests ($p = 0.0001$).

However, the further category X orientation interaction [F(1, 31) = 6.257, $p = 0.018$] indicated that the P300 was larger in response to down than up stimuli only for the body (down: 7.04 µV, SE = 0.60; up: 6.10 µV, SE = 0.67; $p = 0.001$) but not cubes ($p = 0.87$).

Furthermore, the triple category X orientation X attention interaction [F(1, 31) = 4.897, $p = 0.034$] revealed that the larger P300 in response to down (than up) body was significant only for target (down: 10.63 µV, SE = 0.77, up: 9.28 µV, SE = 0.85; $p = 0.0005$)

than non-target ($p = 0.51$) stimuli. No difference was instead found for the cubes (target: $p = 1.00$; non-target: $p = 0.89$). See Figure 2.13, Figure 2.14, and Figure 2.15.

Lastly, these body-related modulation of the P300 was found over all three electrode sites ($p = 0.0002$), as shown by the quadruple category X orientation X attention X electrode interaction [F(2, 62) = 3.862, $p = 0.026$].

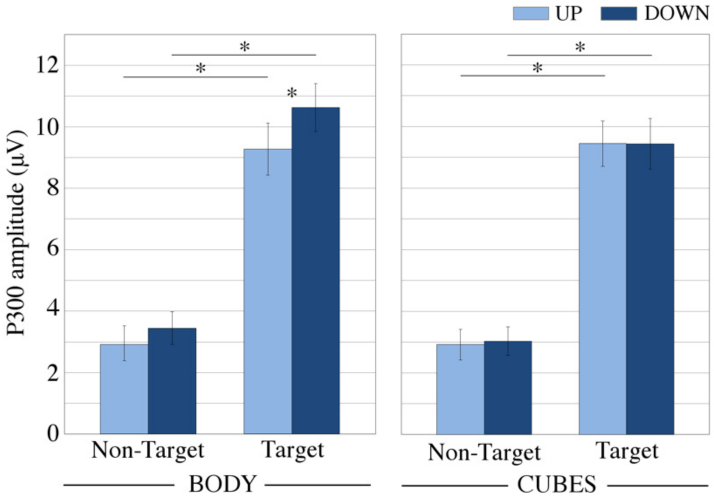


Figure 2.13. Amplitude values of the P300 component. The histogram shows the amplitude values (µV) of the P300 component recorded over centro-parietal sites as a function of the category, attention and orientation factors. The P300 potential was larger in response to target than non-target stimuli in both body and cubes categories. Moreover, upside-down bodies evoked a larger positivity when compared with upright bodies. No difference was shown for the cubes.

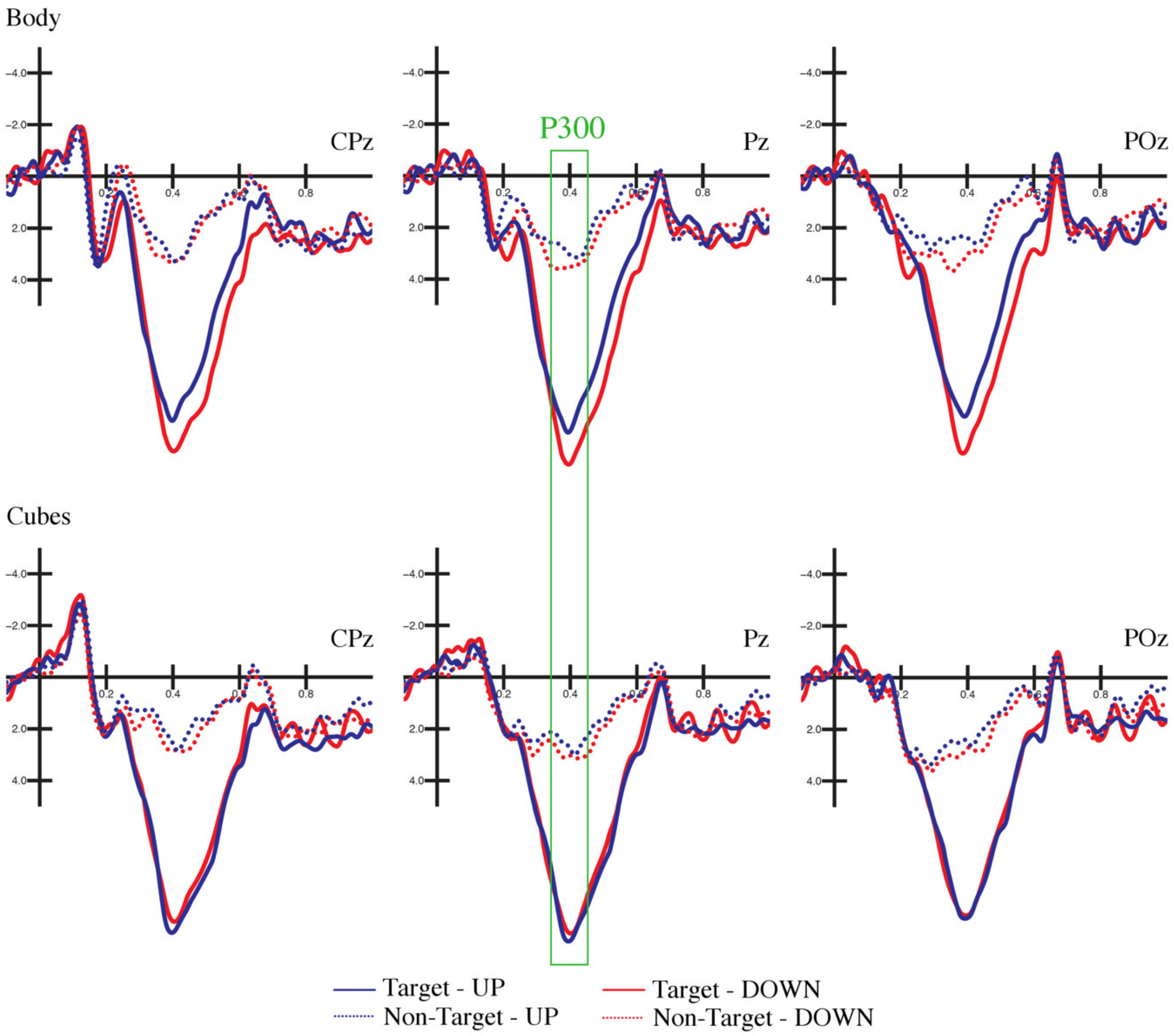


Figure 2.14. Grand average waveforms recorded at centro-parietal sites. Grand average waveforms (ERPs) recorded over centro-parietal sites in response to body (top panel) and cubes (lower panel). The solid lines depict ERPs evoked by target stimuli, while dotted lines represent ERPs to non-target stimuli. Upright stimuli (up) are shown in blue and upside-down stimuli (down) in red.

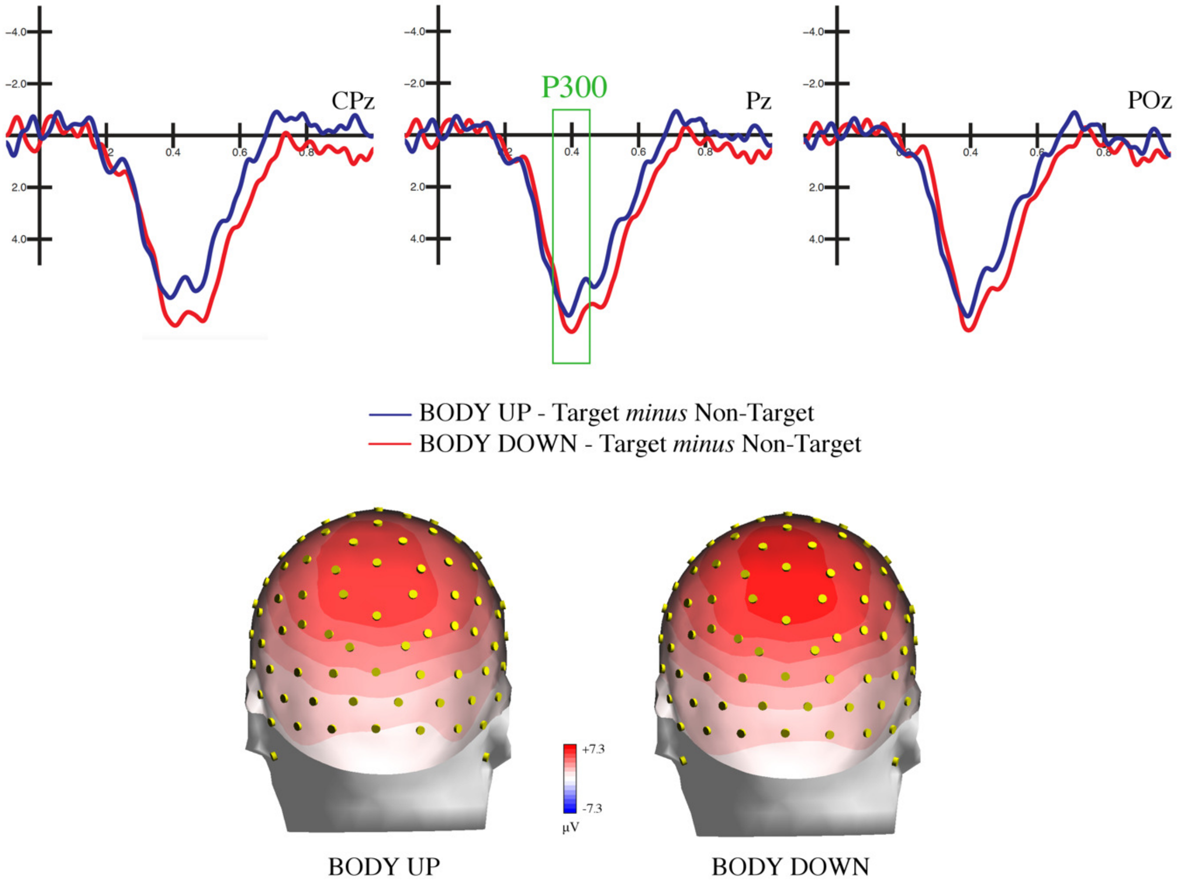


Figure 2.15. Grand averages waveforms (*difference wave*) recorded at centro-parietal sites and topographic map of voltage distribution over the scalp. Grand average waveforms (ERPs) of the *difference wave* target -*minus*- non-target recorded over centro-parietal sites in response to upright body (in blue) and upside-down body (in red). The topographic maps computed over the *difference wave* in the P300 time windows (350-450 ms) show an enhanced response elicited by the upside-down than upright body. The positive values of voltage are shown in red and the negative values in blue.

swLORETA source reconstruction (250-300 ms)

Three swLORETA were performed on the difference waves obtained subtracting ERPs elicited by non-target from those evoked by target stimuli in the SN time window. Specifically, according to the results of the SN-related ANOVA, we reconstructed the neural source in response to upright bodies, upside-down bodies and cubes (regardless of the orientation). 30 ms time window was considered for each reconstruction so that the maximum peak on the grand-average waveforms elicited by targets was included (body up: 235-265 ms; body down: 255-285 ms; cubes: 250-280 ms). Similar active dipoles were estimated by the three reconstructions (see Tables 2.1, 2.2, and 2.3), that included the uncus bilaterally (BA 28/36), right orbitofrontal cortex (BA 11), left anterior prefrontal cortex (BA 10), left middle temporal gyrus (BA 21) and precentral gyrus (BA 6/9). Specifically, enhanced activity was shown in response to inverted than upright bodies. Moreover, the upright bodies also elicited activity in the anterior cingulate cortex (BA 25) and postcentral gyrus (BA 1/2/3), while inverted bodies engaged the right middle temporal (BA 21/22) and precentral gyrus (BA 4/6).

UPRIGHT BODY

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
21.0	1.5	38.2	-17.9	R	F	MedFG	11	Selective attention
17.7	1.5	16.2	-4.5	R	Lim	ACC	25	
16.6	-28.5	46.3	-2.3	L	F	MFG	10	
16.5	-28.5	54.4	15.9	L	F	SFG	10	
19.9	-28.5	-8	-28.9	L	Lim	Uncus	28/36	Affective response
19.6	21.2	-0.6	-28.2	R	Lim	Uncus	28/36	
15.6	-48.5	-36.6	-1.3	L	T	MTG	22	Semantic
6.69	-38.5	2.4	29.4	L	F	Prec Gyrus	6/9	Response
6.28	50.8	-22.5	53.5	R	P	Postc Gyrus	1/2/3	Somatosensory feedback

Table 2.1. List of active electromagnetic dipoles for the upright body. List of active electromagnetic dipoles identified in response to upright bodies according to swLORETA in the SN time window (235-265 ms), with the relative Talairach coordinates. (Legend: Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, Lim – limbic system, Sub – Sublobar, BA - Brodmann Area)

UPSIDE-DOWN BODY

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
23.3	-28.5	-8	-28.9	L	Lim	Uncus	28/36	Affective response
22.4	21.2	-0.6	-28.8	R	Lim	Uncus	28/36	
22.6	-48.5	-36.6	-1.3	L	T	MTG	22	Semantic
16.4	50.8	-26.5	-0.6	R	T	SFG/MTG	21/22	
22.4	1.5	38.2	-17.9	R	F	MedFG	11	Selective attention
22.0	-8.5	57.3	-9	L	F	SFG	10	
17.9	-28.5	54.4	15.9	L	F	SFG	10	
8.5	-38.5	2.4	29.4	L	F	Prec Gyrus/IFG	6/9	Response
5.73	31	-23.2	62.4	R	F	Prec Gyrus	4/6	Mental rotation

Table 2.2. List of active electromagnetic dipoles for the upside-down body. List of active electromagnetic dipoles identified in response to upside-down bodies according to swLORETA in the SN time window (255-285 ms), with the relative Talairach coordinates. (Legend: Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, Lim – limbic system, Sub – Sublobar, BA - Brodmann Area)

CUBES

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
16.2	1.5	38.2	-17.9	R	F	MedFG	11	Selective attention
13.5	1.5	7.2	-12.6	R	F	Subcallosal Gyrus	25	
12.1	-28.5	46.3	-2.3	L	F	MFG	10	
14.8	21.2	-0.6	-28.2	R	Lim	Uncus	28/36	Affective response
14.7	-28.5	-8	-28.9	L	Lim	Uncus	28/36	
13.0	-48.5	-36.6	-1.3	L	T	MTG	22	Semantic
5.80	-38.5	2.4	29.4	L	F	Prec Gyrus	6/9	Response

Table 2.3. List of active electromagnetic dipoles for the cubes. List of active electromagnetic dipoles identified in response to the cubes according to swLORETA in the SN time window (250-280 ms), with the relative Talairach coordinates. (Legend: Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, Lim – limbic system, Sub – Sublobar, BA - Brodmann Area)

2.4. Discussion

Previous evidence has shown reduced recognition ability for bodies presented upside-down (inversion effect) along with increased amplitude and latency of the occipito-temporal N1 component (Reed et al., 2003; 2006; Stekelenburg and de Gelder, 2004). The disruption of configurational body processing has been hypothesized as a result of inverted stimuli presentation. The present study aimed at expanding the existing literature by investigating the role of selective attention and categorization processes in upright and inverted body perception. Thus, the participants were presented with stimuli depicting the shape of a human body and structures of cubes and engaged in a target detection task during EEG recording.

From a behavioral perspective, our data showed that the volunteers recognized more easily the body shape than the cubes, as indicated by the faster RTs and higher accuracy in response to bodies. Moreover, discrimination ability was reduced for inverted than upright bodies, while no difference was visible for cubes as a function of the orientation. These results were concordant with classical evidence on BIE (body inversion effect) that showed increased discrimination ability for bodies than real objects (i.e., houses, animals) and decreased performance when the body (but not object) was presented upside-down (Minnebusch et al., 2008; Reed et al., 2003; 2006). Previous studies reported enhanced discrimination ability of animals relative to artificial objects during perceptual, semantic categorization task, suggesting favorited recognition of homomorphic stimuli (New et al., 2007; Proverbio et al., 2007; Zani et al., 2015). Thus, there appeared to be an advantage for body processing relative to cubes category of stimuli.

The analysis of the anterior N2 component seemed to corroborate this idea. On the one hand, non-target stimuli elicited larger negativity than target stimuli in both categories. As expected, this result was consistent with extensive evidence showing reduced N2 for no-go trials compared to go trials, in which the overt or covert response to a stimulus has to be suppressed (Angelini et al., 2015; Patel and Azzam, 2005). Thus, anterior N2 has been classically linked to attentional-related cognitive processes, including motor inhibition, conflict monitoring, detection of novelty or mismatch (Folstein and Van Patten, 2008; Folstein et al., 2008). On the other hand, the N2 elicited by bodies was larger than that evoked by cubes regardless of the targetedness (attentional condition). EEG studies on categorical discrimination (i.e., animals vs. objects) showed modulation of the anterior N2 according to the semantical category of the visual stimulus (Proverbio et al., 2007; Schmitt et al., 2000; 2001). Moreover, reduced N2 (latency and amplitude) at central sites, decreased RT and increased accuracy was shown as a function of the age under visual stimuli categorization (Batty and Taylor, 2002; Mudar et al., 2015). These results suggested that the modulation of the N2 response can be used as an index of stimulus processing. In our study, the N2 was also faster in latency for bodies (248 ms) than cubes (256 ms) under non-target condition, likely indicating earlier automatic processing of bodily than non-bodily information (Thorpe, 1996). The existence of body-selective visual regions (EBA and BFA) in the OTC (Downing et al., 2001; Peelen and Downing, 2005) might account for the present finding. OTC regions also seemed to be involved in action execution and received kinesthetic feedback on the self-executed action (Orlov et al., 2010). Furthermore, a few fMRI studies suggested predisposition of the EBA to supramodal body processing even in the absence of visual experience. Body recognition in the extrastriate cortex was investigated in congenitally blind and sighted individual (Striem-Amit and Amedi, 2014; Kitada et al., 2014). The EBA demonstrated sensitivity to the body shape presented through a sensory-substitution device (visual stimuli converted in a pattern of sounds), during haptic-identification task of hand shape (vs. objects), and not only for visually presented bodies.

In our study, the latency of the N2 was also modulated by BIE, being faster in response to upright (245 ms) than inverted bodies (253 ms), while no modulation was found for cubes. Namely, earlier processing (Batty and Taylor, 2002) of the body shape was shown when presented in its natural orientation relative to unnatural orientation. In similar time window (230-280 ms) the targetedness resulted in opposite modulation of the posterior N2 over occipito-temporal sites. The negativity was larger in response to target than non-target stimuli. Electrophysiological literature has well documented this increased negativity in response to stimuli characterized by specific target features (Hillyard et al., 1998). The difference obtained subtracting ERP evoked by non-target by those elicited by a target is generally referred to as selection negativity (SN). It is an index of selective attention allocation toward specific features of the visual stimulus, including the color, shape, and size (Molholm et al., 2007; Proverbio et al., 2004; Zani and Proverbio, 2003). In this study, larger SN was shown in response to inverted bodies when compared with upright bodies. This was interpreted as an enhanced attentional resource required for the recognition of the body upside-down presented. At the same time, the lack of preferential orientation of cubes was reflected in the absence of SN modulation for upright and inverted non-body stimuli.

In this regard, a few investigations showed that new-borns (2 days old) had a perceptive preference not only towards biological motion (point-light animation) but specifically for upright than upside-down biological motion (Bardi et al., 2014; Simion et al., 2008). These findings might suggest a biological predisposition for the processing of moving bodies that follow the physical constraints of the gravitational field. In the adults, there is evidence of an internal representation of gravity ("representational gravity", Hubbard, 2005) that affects the visual perception of the body (Barra et al., 2017; Lopez et al., 2009), face (Lobmaier and Mast, 2007), and interaction with moving object (Senot et al., 2005). For instance, Barra and colleagues (2017) created images of body posture (plausible in terms of body segment configuration and balance) depicting upright avatar standing of their feet and upside-down avatar sending on their hands (relative to observer's retinal coordinates). The participants were presented with the original and inverted version of the stimuli and instructed to indicate the direction that a ball released by the avatar would take according to the perceived gravity of the image (up vs. down). When the original upright poses were inverted, there was a gravity conflict (loss of balanced) that led to the classical BIE (reduce accuracy and slower RTs). Contrarily, the BIE was reduced by about 70% in response to those postures originally upside-down created (handstand body). The lack of gravity conflict (the pose was balanced in both orientations) allowed the configuration processing of this category of upside-down body. Previously, Lopez and colleagues (2009) showed that the stability judgment of body postures presented in different orientations was affected by the orientation of the observer (vertical or lying on a side). Finally, evidence of the contribution of both visual and embodied expertise in body perception has been provided (Reed et al., 2012). Studies involving expert individuals with refined motor skills showed increased sensitivity in body and action processing due to acquired expertise (Abreu et al., 2008; Calvo-Merino et al., 2010; Orlandi et al., 2017). Specifically, the advantage in recognizing subtle differences between similar actions exhibited by experts was visible only for bodies presented in their natural orientation (Calvo-Merino et al., 2010). The inversion effect impaired the configurational processing of inverted the bodies even in experts, whose performance did not differ from that of non-experts in this orientation.

In the present study, the posterior negativity was larger over the left than the right hemisphere in both attentional conditions. This result was consistent with evidence showing left asymmetry in object-centered attention, discrimination of object features, and local processing in visual information (Georgopoulos et al., 2001; Yamaguchi et al., 2000; Proverbio et al., 1998; 2004). For instance, Proverbio and colleagues (2004) showed increased posterior N2 response over the left hemisphere when the participants detected specific target feature (color or shape) between non-target stimuli. Moreover, we found that the right hemisphere was more engaged for upright stimuli, whether the left hemisphere was equally sensitive to upright and inverted stimuli. This was consistent with findings that showed body-selective visual regions in the OTC bilaterally (Peelen and Downing, 2005), but with the predominance of the right hemisphere (Engell et al., 2014; Ishizu et al., 2010; Pourtois et al., 2007).

At this point, the assumption of top-down modulation of the OTC as a function of body orientation was tested by estimating the neural sources of selective attention. Three source reconstructions (swLORETA) were performed on the difference waves target-minus-nontarget (for upright and inverted bodies and cubes) in SN time windows. Overall, similar brain regions were engaged for bodies and cubes, including the uncus bilaterally (BA 28/36), right orbitofrontal cortex (OFC; BA 11), left anterior prefrontal cortex (aPFC; BA 10), left middle temporal gyrus (MTG; BA 21) and precentral gyrus (BA 6/9). However, the enhanced magnitude of these estimated dipoles was shown when comparing inverted with upright bodies (see Figure 2.16). As part of the anterior parahippocampal cortex, the uncus is included in the human affective system (Patterson and Schmidt, 2003) and showed strong interhemispheric connections including those with the OFC (Frey and Petrides, 2002; Zeidmann et al., 2015). The activity of this region has been previously shown during the perception of incongruent stimuli representing the human body (Proverbio et al., 2017; Vocks et al., 2010c). At the same time, the OFC has a role in affective regulation and motivation (Arnsten and Rubia, 2012), but also response inhibition, flexible associative encoding, and value-based decision masking (Stalnaker et al., 2015; Wallis, 2012). In the present study, the activity in these limbic/prefrontal regions might suggest an affective response to the norm violation, since the greater engagement during the observation of the inverted than canonical-oriented bodies. Moreover, the aPFC was likely involved in the maintenance of the mental image of the target and its comparison with the incoming stimulus. Activity in the aPFC was previously found during a task requiring updating working memory and prospective memory (Benoit et al., 2011; Halahalli et al., 2015). Moreover, the left MTG is known as a key region in amodal semantic brain network (Fairhall and Caramazza, 2013; Visser et al., 2012; Whitney et al., 2010). Thus, its engagement may result from the semantic categorization of the stimuli. Finally, the precentral gyrus (BA 6/9) was likely involved in the motor selection of the key-press response (Mostofsky and Simmonds, 2008).

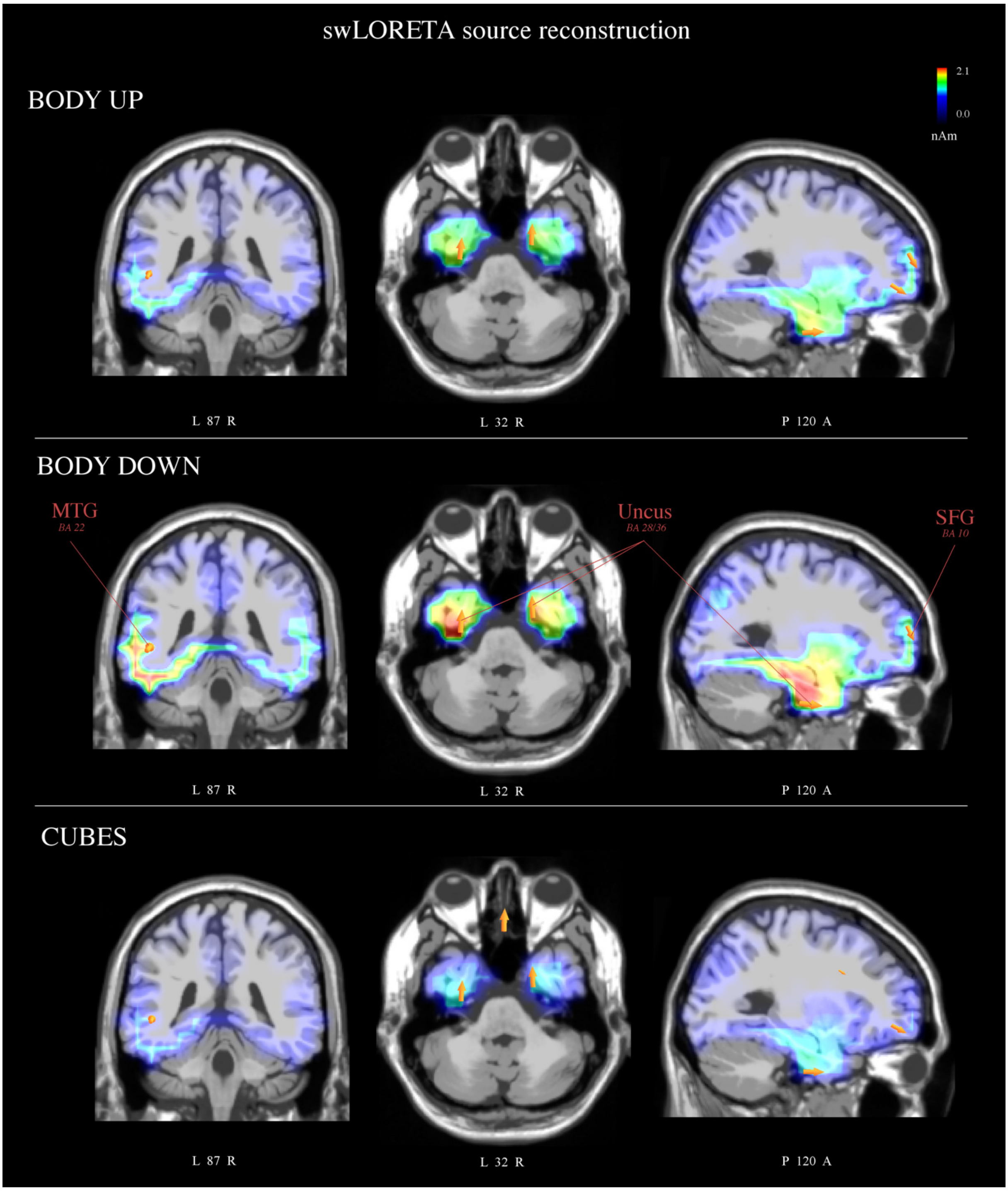


Figure 2.16. SwLORETA source reconstruction of surface potentials in the SN time windows. SwLORETA performed on the grand-average waveforms (in the SN time windows ≈250-280 ms) elicited by the upright body (top panel), upside-down body (middle panel), and cubes (lower panel). The coronal, axial and sagittal anatomical planes of the brain are shown. The activation of the left middle temporal gyrus (BA 22), uncus bilaterally (BA 28/36), and superior frontal gyrus (BA 10) is visible in all the categories. The dipoles were more active in upside-down body condition than upright body condition and cubes. The strongest magnitude values of the signal (nAm) are presented in red.

Besides these similarities, specific dipoles were estimated according to stimulus category and orientation. For instance, cubes and upright bodies engaged the subgenual area (BA 25), region linked to emotional behavior (Drevets et al., 2008), while inverted bodies activated the middle temporal gyrus bilaterally. Moreover, whether the postcentral gyrus (BA 1/2/3) was engaged by upright bodies, the precentral gyrus (BA 4/6) showed activity for theinverted bodies. Thus, naturally oriented body postures elicited some sort feedback in the somatosensory regions (Fiorio and Haggard, 2005), while inverted postures likely required mental rotation as suggested by the activity of the dorsal premotor cortex (de Lange et al., 2006).

Finally, in this study modulation of the parietal P300 by targetedness of the stimuli was shown as well, being larger in response to targets than non-targets. This positivity was classically associated with the updating the mental representation of stimulus context, categorization, and visual awareness (Picton et al., 1992; Polich, 2007). The P300 showed to be sensitive and thus modulated by attention allocation, task difficulty, stimulus complexity, and the probability of occurrence. Here, the target-related P300 showed modulation as a function of stimulus category and orientation. Larger positivity was elicited by inverted relative to upright bodies, but not cubes. On the one hand, an interpretation of this result may appear counterintuitive since the P300 was previously reported as maximal in response to stimuli that were identical to a target (Azizian et al., 2006). Non-target stimuli that shared some of the visual features of the target stimulus elicited a gradient of increasing P300 as a function of increased similarity. In the present study, the recognition of the inverted body required mental rotation processes to realign the perceived stimulus with the neural representation of the canonical-oriented body shape (Bonda et al., 1995). The target categorization would result from the subsequent comparison between the mentally rotated stimulus and body representation.

Previous evidence has shown increased P300 amplitude during decision-making as a function of increasing attention allocation (Rodlo et al., 2001). For instance, Rodlo and colleagues (2001) presented baseball players varying in expertise with videos of pitch throws and asked them to predict the outcome (fastball or curveball) by keypress. Intermediate skill-level participants showed a larger P300 in response to curveball than the advanced skill-level group, together with slower RTs. These findings were interpreted as less efficient decision-making processes as a result of more limited attentional capacity in non-expert than expert observers. Similarly, enhanced P300 was found in response to stimuli characterized by intrinsic affective value during categorization tasks and interpreted as an index of enhanced automatic attentional allocation. For instance, self-relevant stimuli (i.e., self-name or self-face) elicited a larger P300 than familiar and unfamiliar stimuli (Tacikowski and Nowicka, 2010). Also, a more positive P300 was elicited by perceptual targets (red words) than non-target (black words), but also by autobiographical non-target (Gray et al., 2004). Contrarily, a smaller P300 was found during dual-task experiments as a result of divided attentional recourses (Watter et al., 2002). Investigation of clinical population suffering from attentional disorder (i.e., ADHD) also showed reduced P300 amplitude and increased P300 latency in response to target stimuli when compared with non-clinical controls (Szuromi et al., 2011). Therefore, it is possible that BIE impaired configurational processing of bodies, resulting in greater attention allocation requirement for local analysis of details, mental rotation, and subsequent stimuli recognition and categorization. This would explain the increased SN on the left hemisphere (greater magnitude of the active dipoles) and subsequent larger P300 component in response to inverted body shape.

In conclusion, the present study shows evidence of an orientation-dependent recognition of the human body. The faster anterior N2 component indicated earlier processing of the bodies naturally-oriented (vs. unnaturally-oriented). Contrarily, the perception of the inverted body shape required increased attention allocation, as indexed by the larger selection negativity and relative enhanced engagement of prefrontal/limbic regions (swLORETA). Moreover, mental rotation processes were likely required by the categorization of the upside-down but not upright body. This possibly led to the slower reaction times and reduced accuracy found in response to this category of targets. Also, it might explain the larger P300 in response to the inverted bodies. At the same time, the lack of natural orientation of the structures of cubes was reflected by the absence of ERPs modulation as a function of the orientation.

Chapter 3

Muscular effort coding in action representation: an ERP study on observation and imagination of dance kinematics

«Dance, dance, otherwise we are lost»

Pina Bausch

3.1. Introduction

The aim of the present chapter was to investigate the muscular effort encoding in action representation. The effort is here intended as the amount of force exerted during a movement (Chiu, 2018). The number and type of muscle fibers and motor units recruited by action execution vary as a function of the required force. Increased heart rate and blood pressure are also shown during muscle contraction (Gladwell and Coote, 2004). The modulation of muscular effort was extensively used in behavioral, TMS and imaging studies as a tool to investigate the role of premotor and motor region in action representation. In this regard, a few physiological studies have demonstrated that the observation and imagination of simple effortful action (i.e., running, lifting heavy objects) compared with less tiring action led to increased autonomic functions (ANS, autonomic nervous system). For instance, enhanced breath and heart rate was found while individuals were observing (Paccalin et al., 2000) and mental simulating (Decety et al., 1991) locomotion on a treadmill at increasing speed. Similar results were shown while individuals were observing heavy than light object lifting (Paccalin et al., 2000) or imaging pressing and releasing a footplate loaded with different weights (Decety et al., 1993). This evidence was interpreted as an index of metabolic needs anticipation required by motor planning. More recently, increased arterial pressure (AP) and heart rate was shown during MI of effortful trunk or leg movements against gravity, but not effortless horizontal movements of the wrist (Demougeot et al., 2009). At the same time, same action execution led to different modulation of the AP depending on the actual effector (orthostatic hypotension phenomenon). This result suggested that general and aspecific anticipatory central mechanism may prepare the organism for the forthcoming effortful motor task, thought the activity of the ANS. Finally, Kilteny and colleagues (2018) confirmed functional equivalence between MI and real action execution, by showing that MI of finger pressing led to an attenuation of self-touch comparable (in magnitude and spatio-temporal organization) with that of actual movement. Thus, MI recruited the same forward models to predict the sensory consequence of the imagined action.

Specific recruitment of motor regions in effort encoding during action observation has been found by many TMS studies. Alaerts and colleagues showed that TMS pulse delivered on M1 during the observation and execution of object grasping and lifting led to modulation of corticospinal excitability as a function of the object weight (Alaerts et al., 2010a). Larger MEPs were evoked by both tasks involving heavy than a light object. This modulation was also muscle-specific, elicited by both body and trajectory information, and influenced by expertise (Alaerts et al., 2009; 2010b; 2012; Avenanti et al., 2007; Valchev et al., 2016). This evidence highlighted the role of M1 in muscle-specific and time-dependent effort encoding during action observation. At the same time, the stimulation of IFG (Pobric et al., 2006) and SMA (Zénon et al., 2015) affected the estimation of the weight and effort required by object lifting respectively. Similarly, changes in the MEPs amplitude were found during MI of the finger (Helm et al., 2015) and foot (Kato and Kanosue, 2017) actions as a function of the contraction/effort required. Finally, studies involving MI training (Tatemoto et al., 2017) or skilled experts (Fourkas et al., 2008) suggested that refined and phase-tuned simulation of upper-limb movements required specific cognitive representation. For instance, Fourkas and colleagues (2008) showed that MI of tennis forehand resulted in larger MEPs in professional tennis players when compared to kinematically similar actions (table tennis forehand and golf drive). Contrarily, no difference between action types was found in non-players engaged in the same task.

Also, the engagement of a broader network in effort perception has been found by Proverbio and colleagues (2009). The authors showed evidence of enhanced and automatic recruitment of motor and sensory regions during the observation of images representing dynamic/effortful (i.e., running, jumping) than static/effortless (i.e., reading, eating) actions. During a secondary target detection task, dynamic images elicited larger late positivity (LP) over fronto-centro-parietal sites fo the scalp (350 ms from stimulus onset). The source reconstruction (swLORETA) in the LP time window indicated stronger activity in the EBA, MT (middle temporal), STG, PM, M1, and IFG, that was likely the results of enhanced processing of kinematic information conveyed by the effortful stimuli. Several areas that are generally active during action observation (AON, action observation network) seemed to have a specific role in the muscular effort encoding.

A different perspective was proposed by Mizuguchi and colleagues (2016), that presented the participants with videos of slim and fit actors executing dumbbell curls using different weights. When comparing different effort conditions, modulated activity was found in the TPJ and STS, but not any other regions of the AON (i.e., premotor or parietal areas). Thus, the authors suggested engagement of the mentalizing system (of which TPJ is a core region) and not AON/MNS in understanding the effort of an action. In our opinion, the reduced number of stimuli used, and the passive observation task may partially explain this result. Moreover, watching the slim actor lifting the heavy weight may have evoked feelings (i.e., worry) of him getting hurt, instead of effort coding.

An extensive literature on action observation provided evidence of hierarchically and functionally organized processes distributed over interconnected cortical areas (Action observation Network, AON) as a neural substrate for action representation (Grafton and Hamilton, 2007). However, the specific contribution of these regions in the processing of different action features, including the muscular effort, remains still a matter of investigation. Another open question concerns the effect of expertise in modulating the encoding of these specific elements of action (i.e., effort, acceleration, speed). In this regard, several pieces of evidence have shown more focused and efficient activity in the brains of experts when compared with non-experts during action observation (Babiloni et al., 2010), execution (Pau et al., 2013) and motor imagery (Olsson et al., 2008; Wei and Luo, 2010). Perfected capability to read body-related information was also shown in high skilled athletes during mental simulation of the outcome of an action (Abreu et al., 2012; Aglioti et al., 2008). Overall, the actual findings indicated a fine-tuning of visuomotor and body-related regions in experts when compared with non-experts. At the same time, contradicting evidence has been provided on the expertise-related engagement of these areas. For instance, no difference in the LOCT (lateral occipito-temporal cortex) activity has been found when the brain activity of professional dancers and non-dancers was compared during the observation and MI of trained and untrained dance sequences (Di Nota et al., 2016).

In the present study, we compared groups of participants that differed in their expertise level with the observed action. Expert and non-expert ballet dancers were engaged in a motor imagery training and subsequently presented with technical ballet steps during EEG recording. Especially, kinematic information conveyed by the moving body were modulated by focussing on the muscular effort required to reproduce dance steps. Thus, effortful and effortless technical gestures were presented to the participants, who were instructed to mentally reproduce each movement after the observation. According to previous literature, we hypostatized to find a strong impact of dance expertise on action representation. A refined encoding of effort information was expected in experts since their pre-existing cortical representation (motor knowledge) of the gesture developed over the years by motor practice.

Firstly, we investigated the early response of the occipito-temporal regions (OTC) to action observation as a function of expertise. The higher temporal resolution of the EEG/ERP technique than fMRI might lead to useful insights about the open issue on the relationship between expertise and LOCT activity (Di Nota et al., 2016). Regardless of the motor content of the action (effort), we expected an expertise-related difference also at this stage of action processing. In this regard, a few pieces of evidence have shown the enhanced amplitude of the early N1 and N2 visual components as a function of increased visual and sensorimotor expertise with the observed stimuli (Patston et al., 2007; Scott et al., 2006; 2008). Increased functional symmetry in experts has also been shown (Proverbio et al., 2013; Tanaka et al., 2006). For instance, Proverbio and colleagues (2013) found bilateral N1 in response to target words and music scores in musicians but not controls. The non-experts showed left-lateralized component in response to words and relative activity in the left FG only (as estimated by the source reconstruction). This result was interpreted as an index of reduced lateralization of cognitive function as a result of intense visuomotor practice. Thus, we hypostatized that extensive dance practice may have led to reduced asymmetries in the early OTC response (N2) in the brains of dancers but not controls. We also performed a swLORETA source reconstruction to localize the neural generators of the N2 component, expecting bilateral activation in the OTC in dancers only. The occipito-temporal P2 and fronto-central P300 were also measured to investigate possible effect of dance training on stimulus processing (Thorpe et al., 1996; Yang et al., 2012) and categorization (Jin et al., 2011; Polich, 2007) respectively.

Secondarily, taking into account the motor content the gesture (effort), we expected to find refined ability to codify effort information in ballet experts through a recalling of the relative motor programs (Cross et al., 2006, 2009; Orgs et al., 2008). Specifically, for the observation/encoding phase, modulation of frontal positivity was hypostatized in dancers as a function of the effort represented (effortful vs. effortless steps). A larger positive potential was previously reported over frontal sites evoked by stimuli that were subsequently recognized and remembered, suggesting better encoding processes (Dolcos and Cabeza, 2002; Mangels et al., 2001). Contrarily, modulation of late positivity (LP) over posterior sites was expected in non-dancers, as a result of increased kinematic information to encode. In this regard, the information content of a stimulus has been previously associated with modulation of the LP (Bradley et al., 2007), whether it is an emotional (Bayer and Schacht, 2014), semantic (Sitnikova et al., 2003, 2008) or motor-related (Proverbio et al., 2009) content.

For the motor imagery phase, we expected to find a negative potential over anterior sites of the scalp. Previous EEG studies showed engagement of centro-frontal brain regions during MI of complex action that didn't require specific expertise to be reproduced (Cebolla et al., 2015; Weber et al., 2016). We speculated that the level of expertise (Fourkas et al., 2008) and motor content might modulate this component. Moreover, different swLORETA source reconstructions were performed to estimate the intracranial generators of the ERP components of interest. Overall, engagement of fronto-parietal sensorimotor and body-related regions was expected in experts during both phases of the study. Contrarily, enhanced activity in visual and working memory prefrontal regions was expected in control, suggesting an increased cognitive load for individuals lacking cortical motor representation (Pau et al., 2013; Wei and Lou, 2010).

The study has been conducted at the Cognitive Electrophysiology lab (ERP lab) of the University of Milano-Bicocca under the supervision of the Prof. Alice Mado Proverbio.

3.2. Methods

3.2.1. Participants

Thirty-four right-handed female volunteers participated in the present investigation. Specifically, 17 of them were professional ballet dancers between 20 and 42 years of age (mean age: 25.59, SD = 5.29). They all had a formal (professional) dance training in ballet (mean training: 8.88 years, SD = 2.80) and the mean age of acquisition (years when they started studying dance) was 5 years (D = 1.92). They had an actual job dancer and teacher and, overall, acquired expertise with the dance of 20 years (SD = 5.69). The other 17 participants were control University students between 22 and 30 years of age (mean age: 24.88, SD = 2.78) with no experience whatsoever with dance, gymnastics or martial arts (see Table 3.1 for a detailed demographic information about the participants). To avoid an unpredictable, confound of opposite- vs. own-sex effects (during body perception) participants were all females, all right-handed and heterosexual. All the participants had a normal or corrected-to-normal vision and reported no history of neuropsychological disease or drug abuse. The Italian version of the Edinburgh Handedness Inventory was used to assess their right-handedness (experts = 0.74; non-experts = 0.83). The study was approved by the ethical committee of the University of Milano-Bicocca, and all volunteers signed the informed consent before initiating the experiment.

	DANCERS						CONTROLS	
	Age	*Formal education*	*Age of Acquisition*	*Dance training*	*Professional activity*	*Teaching activity*	*Age*	*Formal education*
	20	13	5	15	1	1	30	16
	28	19	6	22	4	4	27	16
	26	13	6	20	8	8	22	13
	27	13	3	24	6	5	30	18
	23	13	10	13	6	1	22	13
	21	13	3	11	3	0	22	13
	22	13	7	15	6	2	22	13
	25	13	6	20	8	5	24	13
	23	13	3	20	1	1.5	22	13
	30	16	5	20	7	3	25	16
	23	16	5	18	4	5	25	16
	22	13	4	18	5	0	24	16
	24	13	4	20	4	0	29	18
	32	13	3	29	6	13	24	16
	23	13	3	20	6	6	26	18
	24	13	6	18	2	0	26	13
	42	13	7	35	30	3	23	13
Mean	**25.59**	**13.71**	**5.06**	**19.88**	**5.91**	**3.38**	**24.88**	**14.82**
SD	**5.29**	**1.92**	**5.69**	**5.59**	**7.33**	**3.46**	**2.78**	**1.88**

Table 3.1. 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.

3.2.2. Stimuli Creation

354 color videos were created and used as stimulus material in the present study. Each clip depicted one out of six professional male dancers performing a dance step belonging to ballet technique (common to male and female dancers). An example of stimuli can be appreciated in Figure 3.1. Since the greater skeletal muscle mass reported in male than female individuals (Janssen et al., 2000), all actors were male dancers, thereby maximizing the effort information conveyed by muscle contraction and action kinematics (Alaerts et al., 2010). A larger variety of movements was recorded for this investigation including jumps, turns, and steps. Specifically, the 50% of them required a great amount of physical effort to be reproduced (177 effortful moves), while the other 50% required less effort (177 effortless moves). The recorded steps are listed in Table 3.2. At first, the entire movements were recorded using a Nikon D7000 reflex (with a frame rate of 25fps) to allow a precise and accurate execution. The dancers started with a preparation pose (i.e., in the case of a pirouette: preparation with feet in the fifth position)

and ended with another final pose (feet in fourth final position). The presence of two professional dancers at the same time in the rehearsal room was helpful to discharge a movement in the event of visible technical errors and repeat it multiple times. Thus, the best version of each step was selected in a second phase of the stimuli creation. In this regard, the chosen stimuli were silenced using Adobe Premiere Pro CC 2015 (v. 9.0) and cut so that they lasted 2000 ms. Specifically, the maximum peak of effort (i.e., highest height or larger extension of arms and legs during a jump) was synchronized at 1000 ms in each clip. Then, the previous 1000 ms and following 1000 ms were included to create the final version of the stimulus. The camera was placed on a tripod at a fixed distance from the dancer. It can be moved on the horizontal axis to make sure that the dancer was always performing at the center of the scene. During the recording, the dancers wore adherent dark clothes to maximize the visibility of the muscles, reduce body-related differences in low-level features between dancers, and ensure a good contrast with the light grey floor and background of the (empty) rehearsal room. The lighting condition was kept constant during all the days of recording, ensuring the equiluminance of the stimuli (≅1.75 fL). The ultimate videos had a size of 23 x 32 cm, subtending a visual angle of 15° 18’ x 11° 15’ when displayed during the experiment.

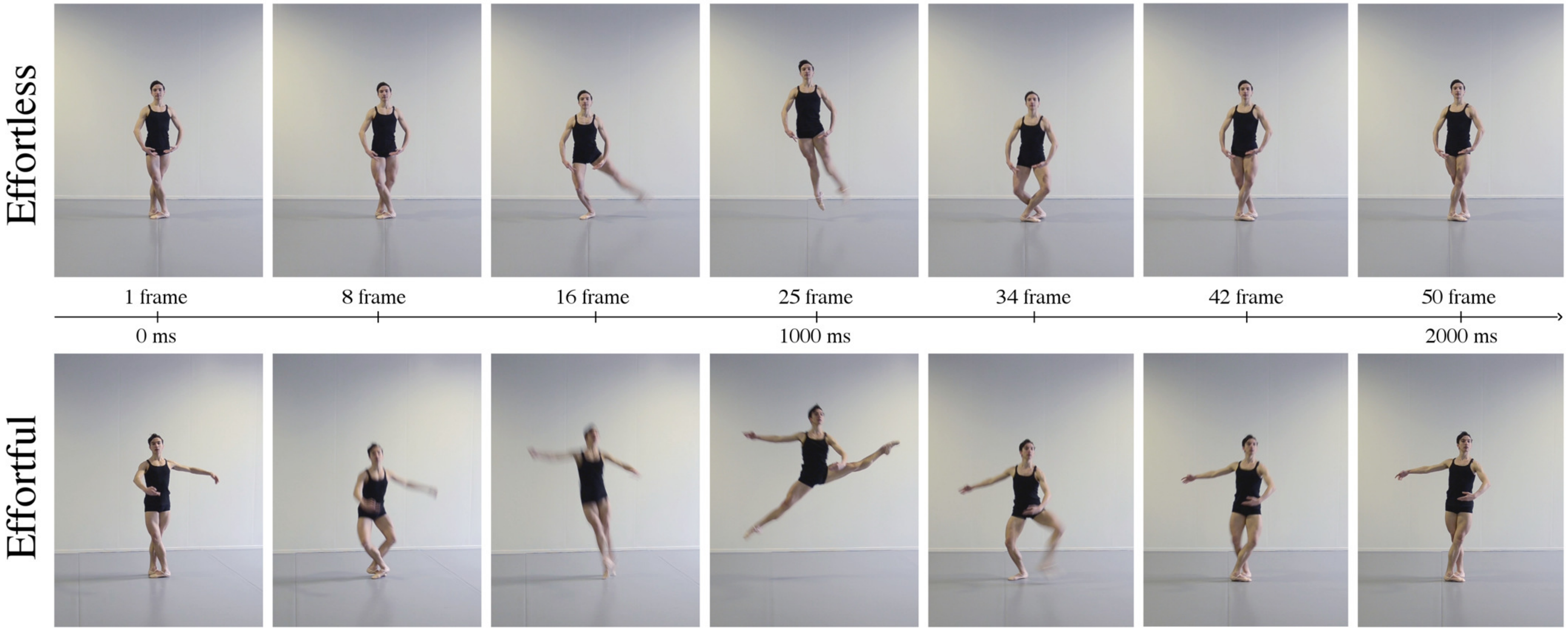


Figure 3.1. Example of stimuli. Seven static frames were taken from each video at different temporal stages and placed side by side to illustrate the difference between the two categories of movement. The upper part of the image shows a step from technical ballet repertoire that requires a moderate effort (effortless): *glissade*. The lower part of the image shows a step that requires a greater muscular effort (effortful): *sissonne*. Information about the exact timing and relative frame is also reported. The maximum peak of effort was synchronized at approximately 1000 ms (25 frames) in all the videos.

Effortful steps	*Effortless steps*
Pirouettes en dedans passé	Pirouette en dedans passé
Pirouettes en dehors passé	Pirouette en dehors passé
Pirouettes en dedans en attitude devant	Pirouette en dedans en attitude devant
Pirouettes en dehors en attitude devant	Pirouette en dehors en attitude devant
Pirouettes en dedans en attitude derrière	Pirouette en dedans sur le cou-de-pied
Pirouettes en dehors en attitude derrière	Pirouette en dehors en attitude derrière
Pirouettes à la seconde	Battement tendu à la seconde
Fouetté	Pirouette en dedans en attitude derrière
Développé >90°	Développé à la seconde à terre
Grand battements en cloche	Battements tendu en cloche
Tours chaînés déboulés vite	Tours chaînés déboulés lents
Sissonne en avant	Pas en avant
Sissonne de côté	Echappé
Sissonne changé	Glissade en avant
Brisé	Assemblé
Brisé volé	Arabesque croisée
Grand assemblé en tournant	Pas de bourrée
Entrechat six	Changement de pieds
Temps levé	Chassé
Renversé sauté	Port de bras
Rond sauté	Rond de jambe à terre en dehors
Entrelacé	Développé arabesque
Grand jetè à la seconde	Glissade derrière
Grand jeté en tournant à l’arabesque	Soutenu en tournant
Grand jeté en tournant à l’attitude	Renversé
Cabriole battue derrière	Battement tendu an arrière
Cabriole battue devant	Battement tendu en avant
Saut de basque	Pirouette en dehors sur le cou-de-pied
Rond de jambe en l'air	Rond de jambe à terre en pliè en dedans
Rond en l'air sauté	Rond de jambe à terre en dedans
Battement fondu relevé devant	Battement fondu développé devant
Battement fondu relevé à la seconde	Battement fondu développé à la seconde
Battement fondu relevé derrière	Battement fondu développé derrière
Pirouette piqué en dehors	Chassé en tournant
Pirouette en arabesque 45°	Arabesque ouverte
Saut de chat	Tombé - pas de bourrée
Tour en l'air	Soubresaut
Pas de ciseaux	Rond de jambe en pliè ne dehors
Pas de basque	Soutenu
Pas de chat	Pas de valse en tournant
Penché	Piqué en attitude

Table 3.2. List of movements. The table illustrates the list of technical gestures recorded from 6 professional dancers on the basis of the muscular effort required by the performance. Effortful movements are reported in the left column and effortless movements are reported in the right column.

3.2.3. Stimuli validation

To ensure that the stimuli were correctly classified in the two categories of interest, a validation process was carried out. It was essential to assess whether each movement was perceived as effortful or effortless by expert dancers. Thus, a sample of twenty female judges took part in this validation phase. Specifically, 10 of them were professional dancers and ballet teachers (mean age: 38.9 years, SD = 11.22) with mean expertise of 26 years on average (26.2 years, SD = 8.75). The other 10 participants were non-dancer controls of a similar age (mean age: 39.7, SD = 14.97) and with no experience with dance, gymnastics or martial arts. The volunteers were presented with the 354 videos displayed in a pseudorandomized order at the center of the screen. A PowerPoint presentation was used for this purpose. The participants were instructed to rate the muscular effort required to reproduce each dance step, by verbally indicating their preference on a double option scale (0 = relatively little effort vs. 1 = considerable effort). 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 the 70% of concordance were discarded. On this base, 326 stimuli (163 effortful and 163 effortless) were selected, counterbalanced for kinematics and space parameters, and used in the present investigation.

Besides, we compared the capability of expert and non-expert judges to perceive and estimate the effort of the dance actions. For each participant, rating scores were averaged to obtain a mean value for effortful and effortless categories of movement. A repeated measure ANOVA with one between-groups factor (group: experts, non-experts) and one within-groups factor (effort: effortful, effortless) was performed on the individual ratings of perceived effort. The significance of the effort factor [$F(1, 18) = 1550.356$, $p < 0.0001$] showed a higher rate in response to effortful (0.87, SE = 0.018) than effortless (0.11, SE = 0.019) stimuli. The further effort X group interaction [$F(1, 18) = 8.896$, $p < 0.01$] and relative Fisher's LSD post-hoc test indicated a significant group-related difference in rating scores of effortful movements (experts: 0.92, SE = 0.02; non-experts: 0.83, SE = 0.02; ($p < 0.05$). Conversely, no group difference was found for effortless stimuli ($p = 0.58$). This evidence was interpreted as an index of underestimation of the effort required by the effortful steps in the group of non-experts. The specific motor knowledge of the motor program of a movement seemed to be essential for a more refined perception and estimation of physical information conveyed by the moving body.

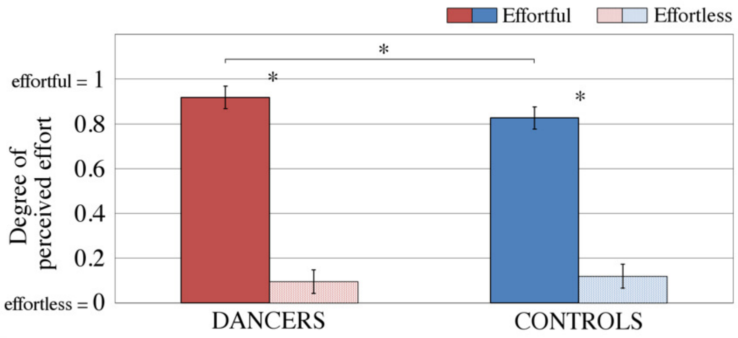
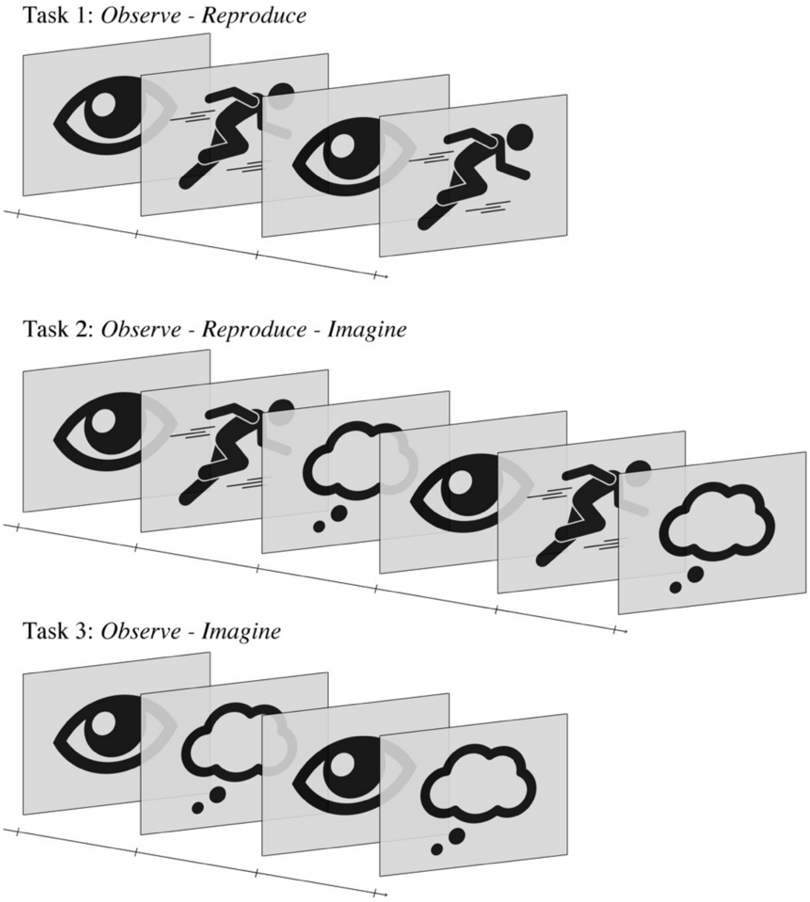


Figure 3.2. Degree of perceived effort. Mean rating values of the perceived effort for the effortful and effortless movements, collected from twenty judges (dancers and controls) during the validation phase. The judges were instructed to categorize each stimulus as effortful (1) or effortless (0).

3.2.4. Task and Procedure

Motor imagery training

After signing the informed consent and compiling the right-handedness questionnaire, participants were engaged in a practical motor imagery training lasting 10-15 minutes. It was essential that all volunteers regardless of dance expertise have a concrete idea and understanding of the meaning of kinesthetic motor imagery. 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, echapee) repertoire. For each action, the volunteers were instructed to perform twice three different tasks (see Figure 3.3). First, they had to observe the experimenter during the execution of the movement and reproduce it as soon as he/she stopped. Second, they had to observe the action, execute it and then imagine reproducing it without any real movement. In this last phase, they were asked to recall all the muscular, sensory and internal bodily sensation occurred during the actual execution on the step. Third, they had to observe the movement of the experimenter and directly imagine reproducing it. The last task also allowed the participants to familiarize with the quite fast timing of the main EEG experiment.



Task 1: *Observe - Reproduce*

Task 2: *Observe - Reproduce - Imagine*

Task 3: *Observe - Imagine*

Figure 3.3. Time scale of the motor imagery training. The volunteers were engaged in three different and consecutive tasks. They were asked to observe the experimenter executing a movement and then: reproduce the same movement (Task 1), reproduce and subsequently mentally simulating the same movement without any actual execution (Task 2), directly simulate the movement (Task 3). The participants were instructed to recall the bodily and kinematic sensation occurred during the reproduction of the action while mentally simulating it.

Procedure

After the imagery training, the EEG-cap was placed on the head of the volunteers; then they were invited to seat in an acoustically and electrically shielded cabin. They were placed 114 cm away from a high-resolution VGA computer screen. To reduce at minimum blinks, eye gazes and body movements they were asked to look at the fixation cross at the center of the monitor, visible for the entire duration of a run. The stimulus material was presented using *Eevoke v2.2* software (ANT, Enschede, The Netherlands). In each trial, a video was presented at the center of the screen (2000 ms), followed by a red fixation cross on a light grey isoluminant background displayed for 900 ± 100 ms (interstimulus interval, ISI). Subsequently, the fixation cross changed color from red to blue and remained visible for 3000 ms (see Figure 3.4). The participants were instructed to observe each video carefully and imagine reproducing the same movement after the color changing of the fixation cross (visual cue for the imagery task). Twelve different runs were created, each lasting 2.88 minutes. The number of effortful and effortless stimuli were counterbalanced within each run, along with the identity of the six dancers in the videos. Moreover, the same dancer was never displayed two time consecutively to avoid any habituation effect due to his identity. Before EEG recording, the volunteers were presented with short training using two additional sequences, composed of the discharged stimuli from the validation phase. Thus, the participants had the opportunity to familiarize with the task and experimental setting. They were all blinded to the aim of the study and stimuli features.

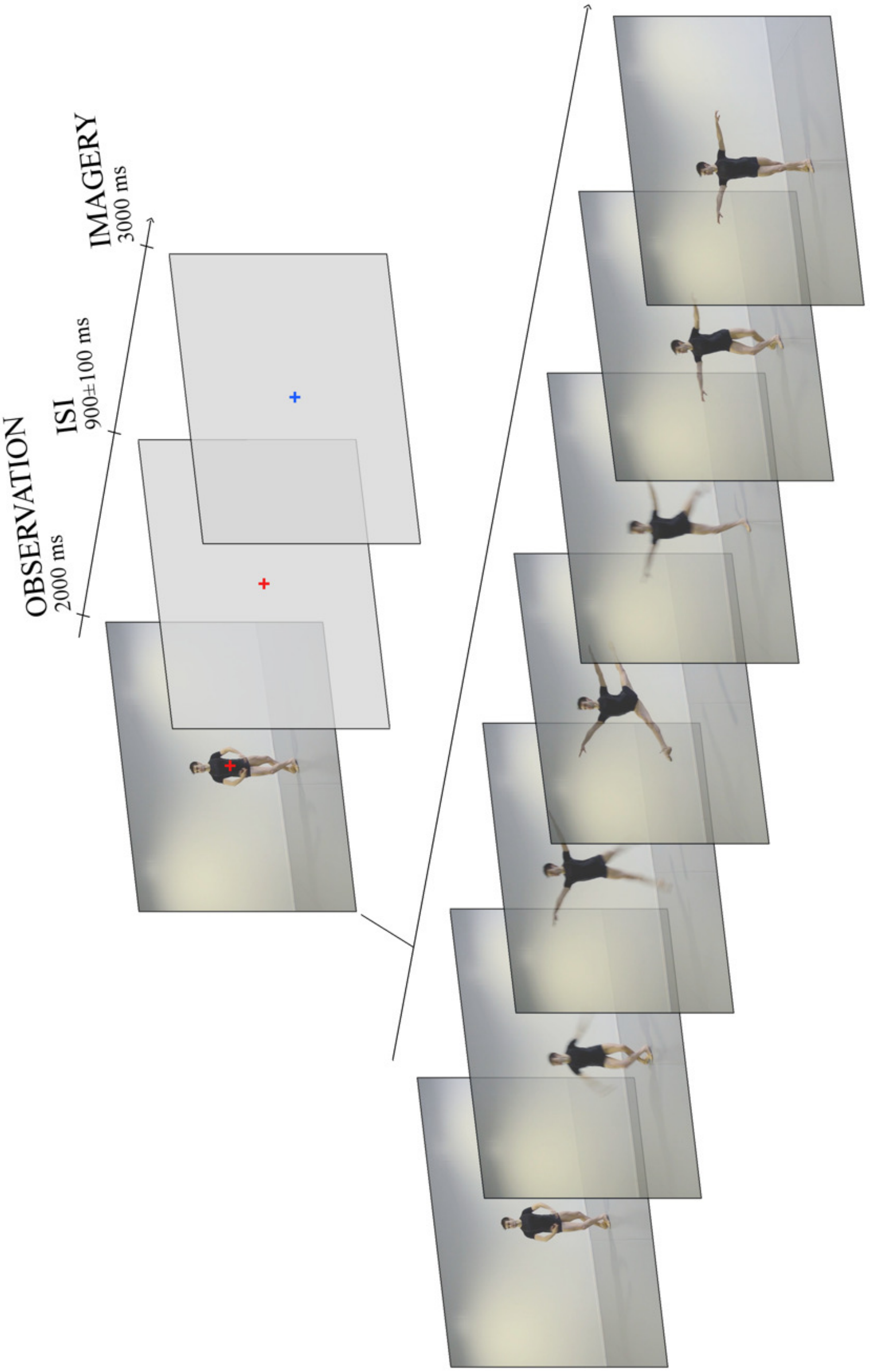


Figure 3.4. Time scale of experimental design. Each video (lasting 2000 ms) was presented at the centre of the screen and followed by a red fixation cross on an isoluminant light grey background. After 900±100 ms (interstimulus interval, ISI) the red cross turned into blue (visual cue), while the background remained the same (3000 ms). The participants were instructed to observe each movement (observation phase) and to kinematically image to perform it (imagery phase), as soon as the fixation cross changed color. Each trial lasted at about 6000 ms.

3.2.5. EEG recording

EEGs were continuously recorded from 128 scalp sites located according to the 10–5 International System (Oostenveld and Praamstra, 2001) at a sampling rate of 512 Hz, using EEProbe v2.2 (ANT software, Enschede, The Netherlands). Horizontal and vertical eye movements were also recorded. Averaged mastoid served as the reference lead. The EEGs and electrooculograms were amplified and filtered with a half-amplitude band-pass of 0.16–70 Hz (notch of 50 Hz). Electrode impedance was kept below 5 kΩ. Computerized artifact rejection was performed before averaging to discard epochs in which eye movements, blinks, excessive muscle potentials, or amplifier blocking occurred. The artifact rejection criterion was based on peak-to-peak amplitudes exceeding 50 μV. For the observation phase, EEG epochs were synchronized with the onset of the video. ERPs were averaged off-line from −100 ms before to 2000 ms after stimulus onset and filtered with a band-pass of 0.016–15 Hz. For the imagination phase, EEG epochs were synchronized with the onset of the color changing of the fixation cross. ERPs were averaged off-line from −100 ms before to 1000 ms after stimulus onset and filtered with a band-pass of 0.016–30 Hz. ERP components were identified and measured with reference to the average baseline voltage calculated over the 100 ms before the stimulus onset at sites and latency when maximum amplitude was reached (Picton et al., 2000) and based on previous literature. ERP averages were computed as a function of group, effort, electrodes, and hemisphere factors.

For greater clarity, data analysis and results of the observation and imagination phases will be presented and discussed separately. Specifically, the first section concerns the expertise-related early modulation response of the occipito-temporal cortex (OTC) regardless of stimuli manipulation. The second section provides evidence of effort coding during the observation of dance actions. The third section includes details about the motor imagery of dance kinematics.

3.3. Perception of dance gesture

3.3.1. Data analysis

The latency and amplitude of the maximum peak of the voltage of the posterior P2 component were measured at TP7, TP8, TPP7h, TTP8h, PO7, and PO8 electrode sites (see Figure 3.5). The latency and amplitude of the maximum peak of the voltage of the occipito-temporal N2 component were measured at TPP9h, TPP10h, P7, P8, PO9, PO10, PPO9H, and PPO10h electrode sites. The mean area voltage of the fronto-central P300 component was measured at Fz, FCz, and Cz electrode sites during the 360-560 ms time window. The ERP data were subjected to multifactorial repeated measures ANOVA (performed using Statistica version 10 software by Statsoft) with one between-groups factor (group: experts, non-experts) and two within-groups factors, including hemisphere (left, right) and electrode factors (depending on the component). Low-Resolution Electromagnetic Tomography (LORETA) was applied to the ERPs elicited during stimuli observation between 240-300 ms in both groups of participants.

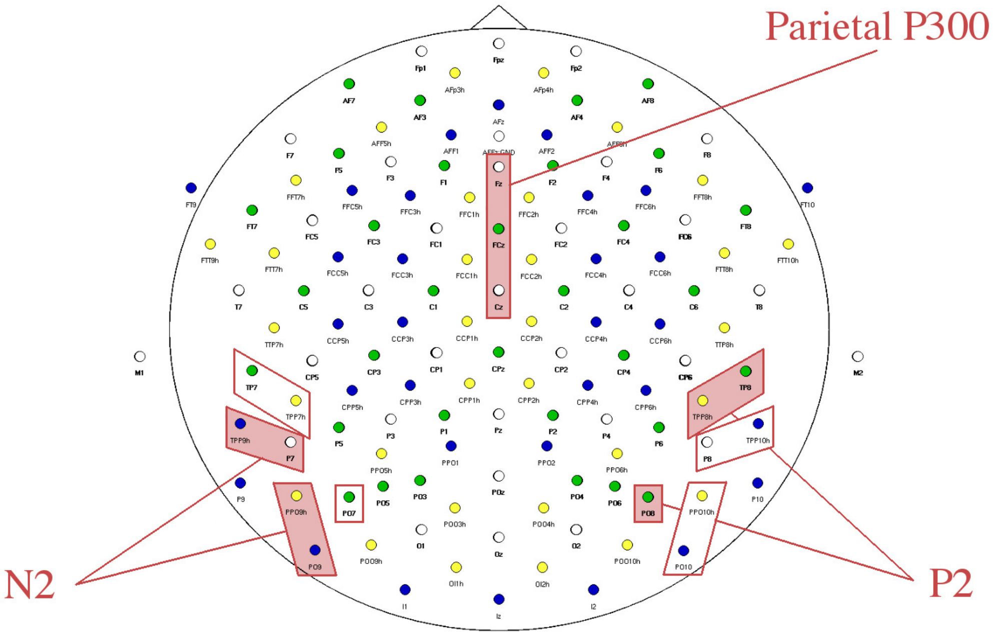


Figure 3.5. Schematic representation of the 128 electrode sites EEG-cap. The figure illustrates the position of the 128 electrodes on the scalp and those selected for the measurement of the three ERP components of interest.

3.3.2. Results

P2 Latency

As can be appreciated in Figure 3.6, the latency of the P2 was modulated by the expertise of the participants. The ANOVA performed on the P2 latency values showed a main effect of the group factor [F(1, 32) = 7.903, $p < 0.01$], as also displayed in Figure 3.7. The P2 response was faster in the dancers (203 ms, SE = 3.83) than controls (218 ms, SE = 3.83). Furthermore, the significant electrode factor [F(2, 64) = 14.162, $p < 0.0001$] and relative post-hoc tests indicated that the P2 was faster over posterior occipito-temporal sites (PO7-PO8: 204 ms, SE = 2.79) than anterior occipito-temporal sites (TPP7h-TPP8h: 211 ms, SE = 2.94, p < 0.003; TP7-TP8: 216 ms, SE = 3.36, p < 0.0001). Finally, the P2 was faster over the right (206 ms, SE = 2.99) than left (214 ms, SE = 3.09) hemisphere, as shown by the significant hemisphere factor [F(1, 32) = 7.963, $p < 0.01$].

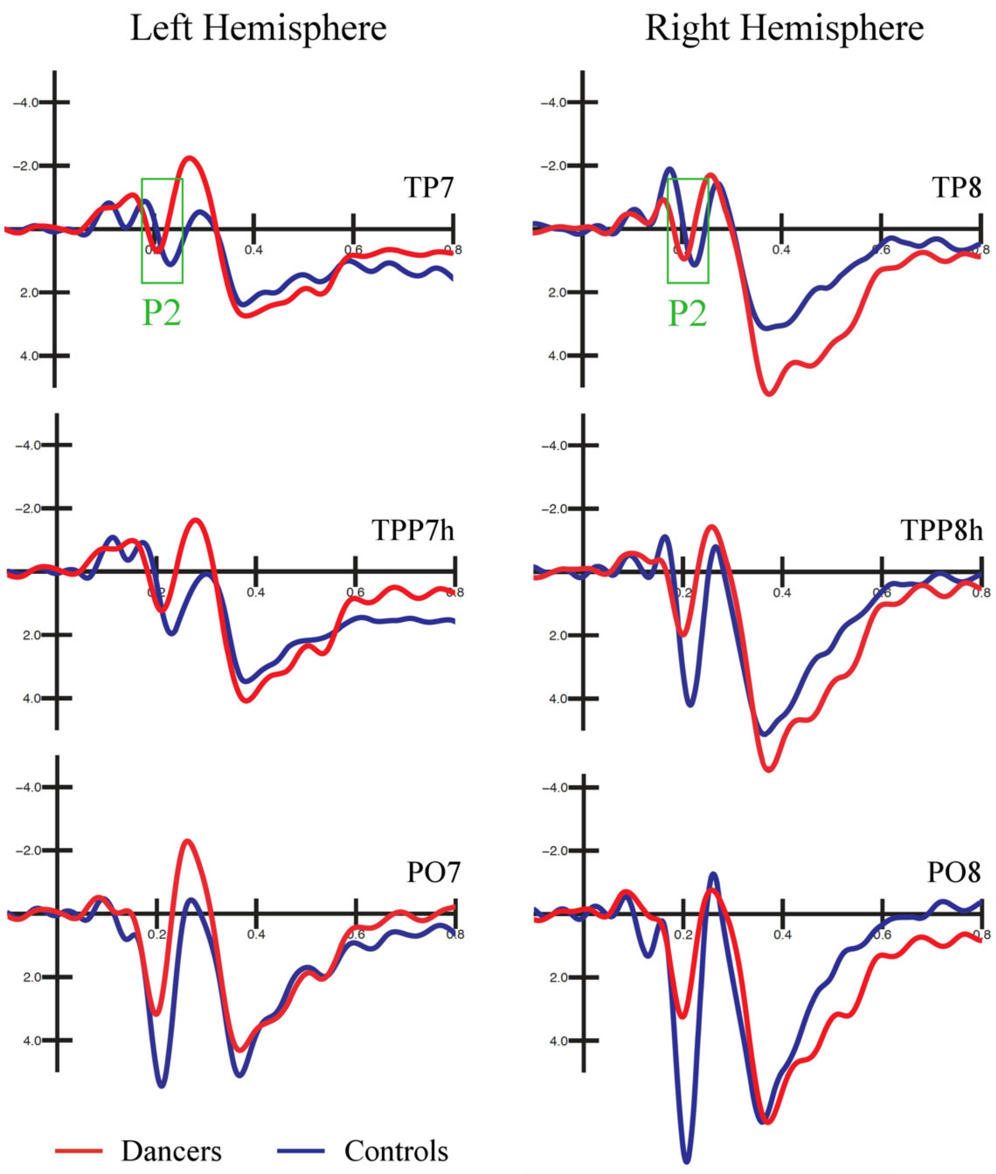


Figure 3.6. Grand average waveforms recorded at occipito-temporal and temporo-parietal sites. Grand average waveforms (ERPs) recorded over occipito-temporal and temporo-parietal sites in dancers (in red) and controls (blue). An early P2 response is visible in the dancers than controls at all electrode sites. A between-group difference in the P2 amplitude was also found at PO7-PO8 electrode sites, being larger in the controls than dancers.

P2 Amplitude

The ANOVA performed on the P2 amplitude values showed the significance of the electrode factor [F(2, 64) = 66.402, $p < 0.0001$]. The P2 component was larger over posterior occipito-temporal sites (PO7-PO8: 5.62 μV, SE = 0.47) than anterior occipito-temporal sites (TPP7h-TPP8h: 2.99 μV, SE = 0.32; TP7-TP8 (1.49 μV, SE = 0.25). The relative post-hoc tests showed a significant difference between all electrode sites (p < 0.001). The further group X electrode interaction [F(2, 64) = 6.054, $p < 0.01$] and relative post-hoc comparisons confirmed the former difference in both group of participants (see Figure 3.7). More importantly, the P2 was larger in controls (6.88 μV, SE = 0.67) than dancers (4.36 μV, SE = 0.67) only over the posterior sites (PO7-PO8: p < 0.001), but not anterior sites (TP7-TP8: p = 0.88; TPP7h-TPP8h: p = 0.37). The significant electrode X hemisphere interaction [F(2, 64) = 3.753, $p < 0.03$] also showed that the P2 was larger over the right than left hemisphere at PO7-PO8 (right: 6.28 μV, SE = 0.71; left: 4.97 μV, SE = 0.55; p < 0.008) and TPP7h-TPP8h (right: 3.79 μV, SE = 0.50; left: 2.19 μV, SE = 0.32; p < 0.002), but not TP7-TP8 (p = 80), as confirmed by the post-hoc tests.

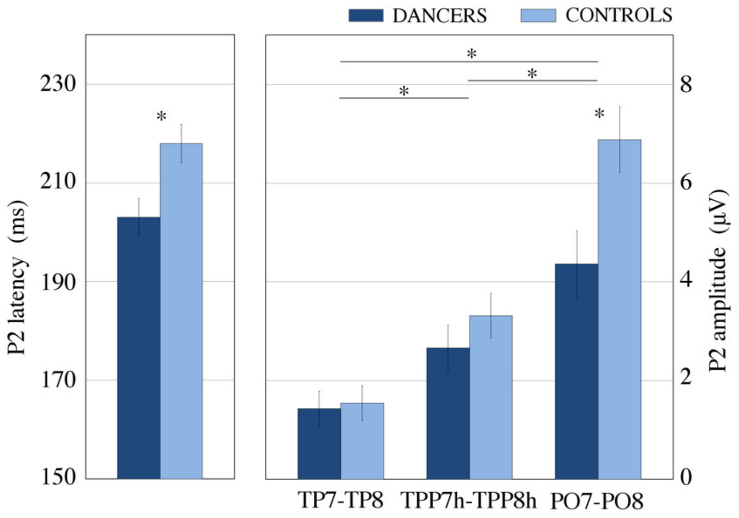


Figure 3.7. Latency and amplitude values of the P2 component. The histogram on the left displays the latency values (ms) of the P2 component recorded over occipito-temporal and temporo-parietal sites as a function of the group factor**.** A larger positivity was shown in the dancers compared with controls. The histogram on the right displays the peak amplitude values (μV) of the P2 component as a function of the group and electrode factors. A larger positivity was found in the control group compared with the dancers' group only over PO7-PO8 electrode sites.

N2 Latency

Repeated measure ANOVA performed on the latency values (ms) of the N2 component showed an earlier negativity over the right (263 ms, SE = 3.09) than left (274 ms, SE = 3.71) hemisphere (see Figure 3.8), as suggested by the significant hemisphere factor [F(1, 32) = 9.800, p = 0.0037].

The electrode factor also reached the statistical significance [F(3, 96) = 6.705, $p < 0.001$], showing a faster N2 over posterior occipito-temporal sites (PO9-PO10: 266 ms, SE = 3.21; PPO9h-PPO10h: 267 ms, SE = 3.12) than anterior occipito-temporal sites (P7-P8: 271 ms, SE = 2.82; TPP9h-TPP10h: 271 ms, SE = 3.01).

Finally, the significant hemisphere X electrode interaction [F(3, 96) = 5.953, $p < 0.001$] and the relative post-doc comparisons indicated that the N2 was overall earlier over the right than left hemisphere at all electrode sites ($p < 0.001$). Moreover, the previously reported difference in latency between electrode sites (posterior vs. anterior) was found only over the left ($p < 0.001$) but not right ($p > 0.50$) hemisphere.

N2 Amplitude

Repeated measure ANOVA performed on the amplitude values (μV) of the N2 component showed a significant group X hemisphere interaction [F(1, 31) = 5.269, $p = 0.029$]. Duncan's post-doc tests suggested that the negativity was larger in experts (-4.44 μV, SE = 0.72) than non-experts (-1.89 μV, SE = 0.70) over the left hemisphere ($p < 0.04$). Contrarily, no group-related difference was found over the right hemisphere (experts: -2.96 μV, SE = 0.66; non-experts: -3.09 μV, SE = 0.64*;* $p = 0.90$). This interaction can be appreciated in Figure 3.9 and Figure 3.10.

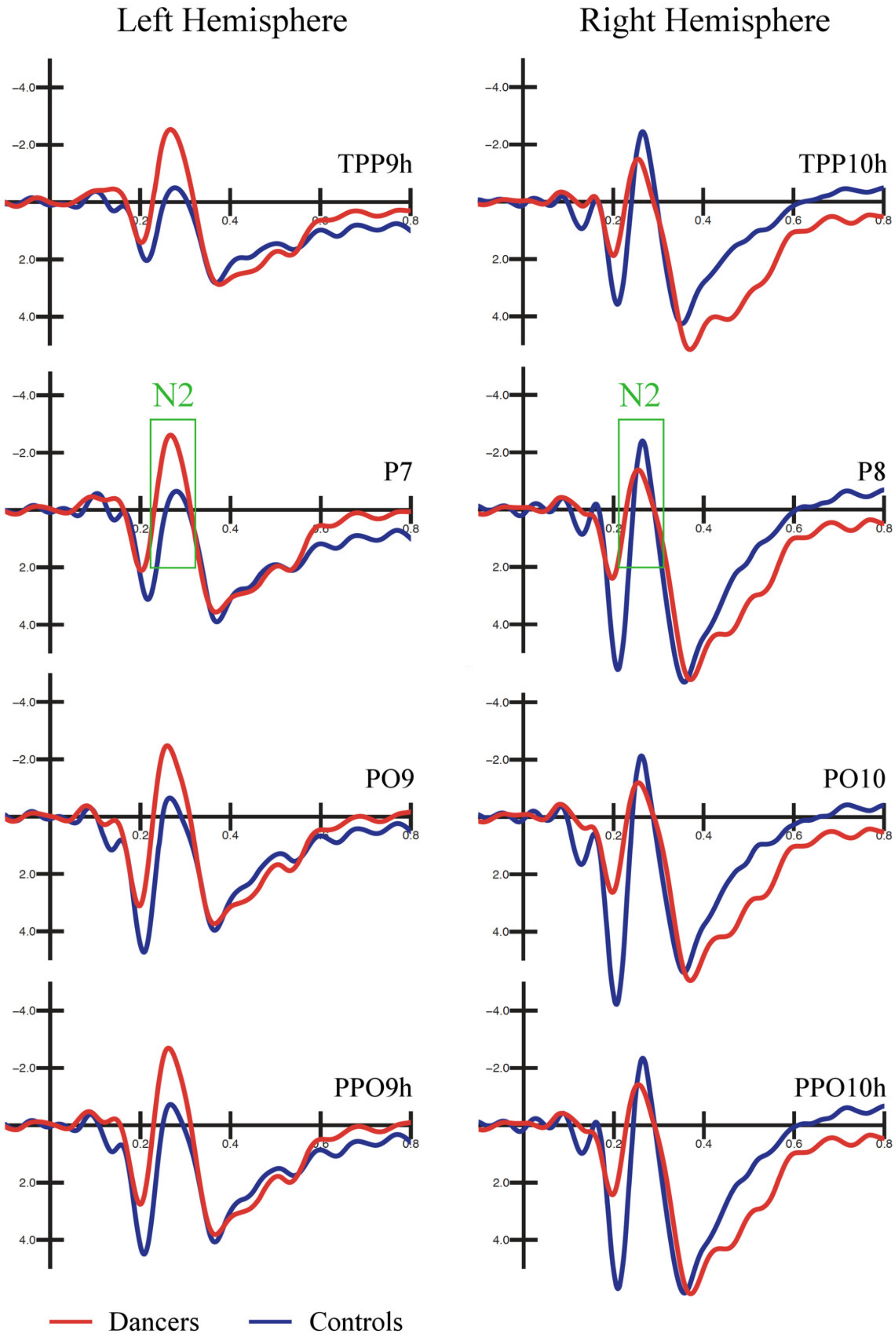


Figure 3.8. Grand average waveforms recorded at occipito-temporal sites. Grand average waveforms (ERPs) recorded over occipito-temporal sites in dancers (in red) and controls (in blue). An expertise-related modulation of the N2 component is visible over the left hemisphere, being larger in the dancers than controls.

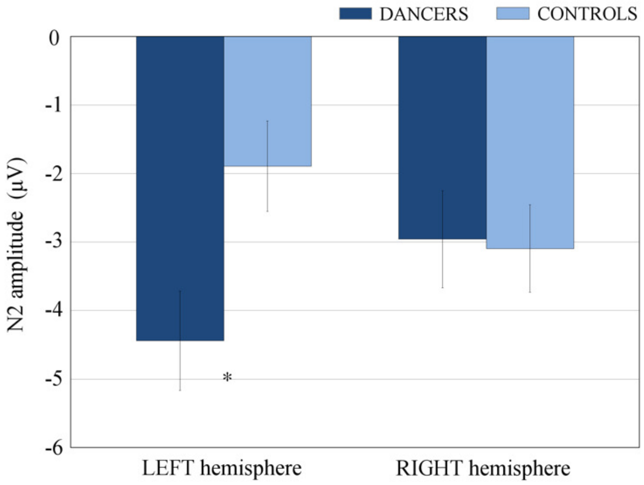


Figure 3.9. Amplitude values of the N2 component. The histogram illustrates the peak amplitude values (µV) of the N2 component recorded at occipito-temporal sites as a function of the hemisphere and group factors. A larger negativity (N2) was found over the left hemisphere in the dancers compared with controls. Contrarily, no expertise-related difference was shown over the right hemisphere.

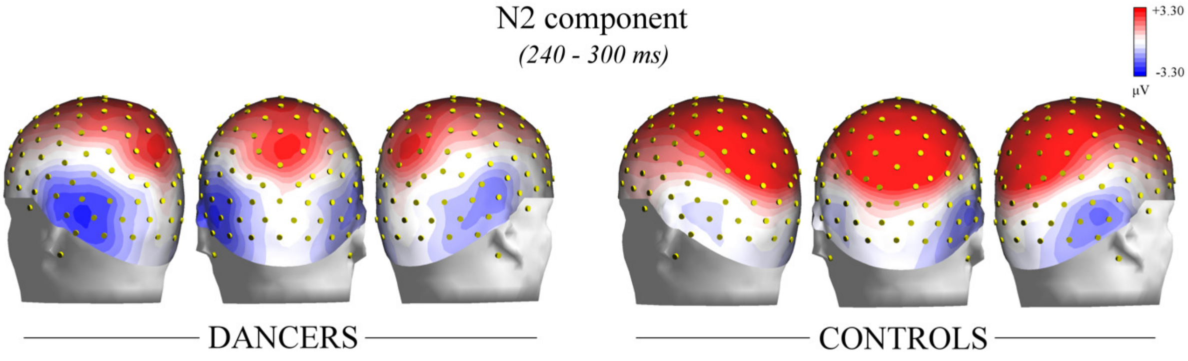


Figure 3.10. Topographic map of voltage distribution over the scalp. The figure illustrates the topographic maps of the scalp voltage distribution computed in the N2 time window (240-300 ms) in dancers (on the left) and controls (on the right). The positive values of voltage are shown in red, and the negative values in blue.

P300 (360-560 ms)

As can be appreciated in Figure 3.11, the fronto-central P300 was modulated by dance expertise. The ANOVA performed on the mean area of the P300 indicated a larger positivity in dancers (3.27 µV, SE = 0.56) than controls (0.96 µV, SE = 0.56), as shown by the significant group factor [F(1, 32) = 8.538, $p < 0.007$]. Moreover, the significant electrode factor [F(2, 64) = 53.058, $p < 0.0001$] and relative post-hoc tests showed that the P300 was larger over central than frontal sites (Cz: 2,99 μV, SE = 0.41; FCz; 2.12 μV, SE = 0.41; Fz: 1.23 μV, SE = 0.41; p < 0.001).

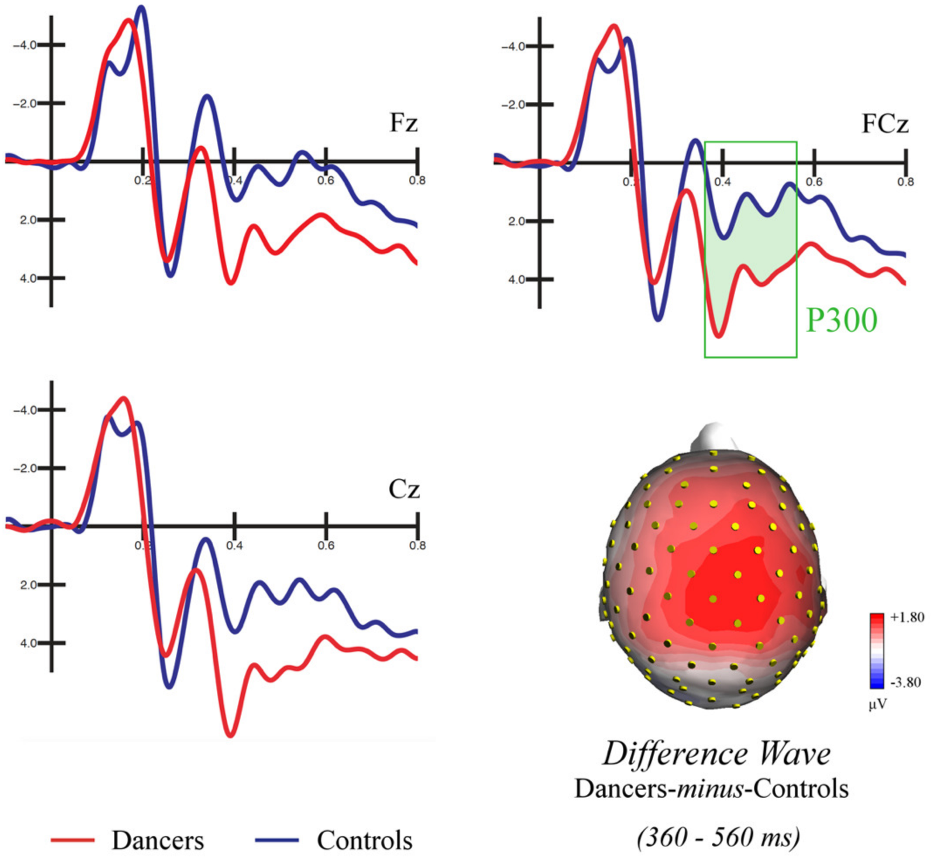


Figure 3.11. Grand average waveforms recorded at fronto-central sites and topographic map of voltage distribution over the scalp. Grand average waveforms (ERPs) recorded over fronto-central sites in dancers (in red) and controls (in blue). An expertise-related modulation of the P300 component is visible over the midline, being larger in the dancers than controls. The topographic map of the scalp voltage distribution computed on the difference wave dancers-*minus*-controls in the P300 time window (360-560 ms) is shown in the bottom-right part of the figure. The positive values of voltage are shown in shades of red.

swLORETA source reconstruction (240-300 ms)

Two swLORETA were performed to estimate the neural sources of the voltage recorded over the scalp in the N2 time window, one for each group of participants. A unique time window was used for these analyses (240-300 ms) to include the peaks over the left and right hemisphere in both groups of experts and non-experts. The main active electromagnetic dipoles included bilateral body- and face-related visual regions: the fusiform gyrus (BA 37/20), middle temporal gyrus (BA 39/21), and cuneus/precuneus (BA 19) in experts (see Table 3.3). Activity was also found in the right fronto-parietal mirror regions (inferior parietal lobule, BA 40 and precentral gyrus, BA 6), superior and medial frontal gyri (BA 9/10) in the brains of dancers. Conversely, the right hemisphere was mainly engaged in the brains of controls, including the cuneus (BA 19), superior and medial frontal areas (BA 10), precentral (BA 6) and left postcentral gyri (BA 3).

DANCERS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
26.69	-48.5	-55.0	-17.6	L	T	FG	37	Body and face related visual regions
25.99	-38.5	-69.0	13.6	L	T	MTG	39	
22.94	-8.5	-81.1	30.6	L	O	Cuneus	19	
22.21	11.3	-82.1	39.5	R	P	Precuneus	19	
18.16	50.8	-33.7	-23.6	R	T	FG	20	
17.76	60.6	-35.7	-8.8	R	T	MTG	21	
18.01	60.6	-39.6	25.1	R	P	IPL	40	Sensorimotor regions
9.47	40.9	2.4	29.4	R	F	Prec Gyrus	6	
15.97	1.5	53.4	24.8	R	F	SFG	9	
15.03	21.2	53.4	24.8	R	F	SFG	9	
13.07	1.5	57.3	-9.0	R	F	MedFG	10	Working memory

CONTROLS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
36.25	11.3	-81.1	30.6	R	O	Cuneus	19	Body and face related visual regions
21.09	11.3	44.4	15.0	R	F	MedFG	10	Working memory
20.58	31.0	54.4	15.9	R	F	SFG	10	
18.75	1.5	57.3	-9.0	R	F	MedFG	10	
14.68	40.9	2.4	29.4	R	F	Prec Gyrus	6	Sensorimotor regions
9.08	-38.5	-21.0	35.7	L	P	Postcl Gyrus	3	

Table 3.3. List of active electromagnetic dipoles. List of active electromagnetic dipoles identified in dancers and controls according to swLORETA in the N2 time windows (240-300 ms), with the relative Talairach coordinates. The strongest sources of activation included the fusiform and middle temporal gyri bilaterally, cuneus/precuneus and right inferior parietal lobule in dancers. The main dipoles in controls were instead localized in the right cuneus and anterior prefrontal cortex. (Legend: Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann Area)

3.3.3. Discussion

One of the aims of the present study was to investigate the impact of dance expertise on the early OTC (occipito-temporal cortex) response during the observation of dance gesture. Therefore, the bioelectrical brain activity of professional ballet dancers and non-dancer controls was compared during action observation. The participants were presented with clips of technical ballet steps and instructed to observe each movement to imagine reproducing it subsequently. The effort manipulation of the stimuli was not considered in this first phase of analysis; thus, the two categories of movements were here collapsed. Pieces of evidence established the presence of visual regions in the OTC sensitive to body, face, object and motion perception (Downing et al., 2001; Peelen and Downing, 2005;). Despite a bilateral activity of the EBA and FBA, these regions are preferentially engaged in the right hemisphere during the observation of body or body parts. Increased expertise with objects or body awareness was previously linked to changes in the response of the OTC (Scott et al., 2006; 2008; Suchan et al., 2010; 2013), especially in the left hemisphere. Moreover, motion (hMT+; Ricciardi et al., 2007) and biological motion (pSTS; Hirai et al., 2003; 2005) sensitive regions were found in the OTC, together with a specific engagement of these areas in action encoding (Ma et al., 2018; Tucciarelli et al., 2015). We hypothesized to find an expertise-related different engagement of the left OTC, indexed by the modulation of the posterior N2 component.

A difference in the amplitude of the N2 component was found, according to the level of dance experience of the volunteers. Specifically, a more negative potential was shown over the left OTC in experts than non-experts. At the same time, no group difference was visible over the right hemisphere. The grand-average waveforms and the maps of topographical distribution in the N2 time window are respectively represented in figure 3.8 and 3.10. A graphical representation of this first set of results can easily be appreciated in them. The N2 component is well-documented in the literature and considered a measure of attentional processes related to the activity of the visual cortex (Anllo-Vento et al., 1998; Zani and Proverbio, 2003). It is generally recorded over posterior electrode sites between 230 and 300 ms from the stimulus onset. It is used to investigate attention allocation in visual search and target detection tasks towards specific features of a stimulus, including the shape, color, and size. In particular, attended targets elicits more negative component that unattended target stimuli. The difference between the ERP evoked by these two conditions (target-*minus*-non-target) gives rise to a difference wave referred to as selection negativity (SN) and interpreted as an index of selective attention.

Previous evidence has shown the role of visual expertise with faces (Tanaka et al., 2006) and objects (Scott et al., 2008) in modulating the amplitude of this negative component. Tanaka and colleagues (2006) compared ERP evoked by the observation of the participants' own face and other unknown faces during a target detection task (specific face). In the first half of the experiment, no difference in the N250 evoked by the target and unknown faces was found. In the second half of the experiment, the repeated exposition to the specific face resulted in a larger N250 (compared with unknown faces) over the left hemisphere, similar to that elicited by the participants' own face. In two studies by Scott and colleagues, participants were trained with pictures of animals (2006) and cars (2008) at basic (category of object) and subordinate (specific elements) level. The participants were engaged in a same-different judgment task during EEG recording. The N2 component was able to discriminate between the two levels of training. It was larger in response to stimuli that undergone the subordinate-level training, requiring more detailed encoding. A follow-up one week apart demonstrated the persistence of this effect, that can be seen as a good index of acquired experience.

A similar impact of visual learning on the representation of objects in the visual regions was shown in an fMRI study by Wong and colleagues (2009). When participants were observing novel abstract objects (*Ziggerins*) after categorization training (basic-level), increased activity was found in the medial regions of the ventral OTC. After individuation training (subordinate-level), enhanced activity was specifically found in the right FG in response to the *Ziggerins*. These results suggested enhanced engagement of the OTC as a result of refined stimuli representation due to acquired expertise. Recently, Folstein and colleagues (2017) hypothesized the existence of two overlapping processes occurring in the N2 time window, indexed by different components. They presented the participants with a category learning training of novel cartoon animals before attending a target detection task. A SN was found between 230-400 ms over posterior site, showing an increasing pattern as a function of the attended features of the stimuli. However, larger negativity was measured in response to trained compared with untrained targets in an early time window (230-315 ms), suggesting a partial dissociation between the expertise-related N250 and attention-related SN.

More importantly, a posterior negative response was found in several investigations on biological motion perception (Hirai et al., 2003; 2005; Krakowski et al., 2011). The latency of this component differed between studies (i.e., 240 ms, 330 ms) but resulted compatible with the time windows of our N2. This negativity was enhanced in response to point-light animations depicting biological motion rather than scrambled motion. Motion-selective attention also enhanced this response, that was bilaterally distributed but with a predominance over the right hemisphere (Hirai et al., 2005). White and colleagues (2014) showed a modulation of the N2 also in response to static human figure, thus interpreting the negativity as an index of shape and action integration. This was consistent with the evidences by Jastorff and Orban (2009), that showed the automatic engagement of the EBA and FBA, even in absence of a task, in response to human shape and action kinematics. The authors suggested a role of these two regions of the OTC in the initial stage of action processing, linking the action to the body of the actor.

In our study, the modulation of the N2 may be linked to increased experience with moving human bodies. The expertise-related difference may be ascribed to the finest capability of experts to encode kinematic information (Calvo-Merino et al., 2010), that allows them to learn sequences of movement in faster and more effective manner. In this regard, several evidences pointed out a role of the OTC in body perception (Taylor et al., 2007; 2010), coupling between limbs shape and kinematics (Orlov et al., 2014), and movement preparation (Astafiev et al., 2004; Kühn et al., 2011). Results from MVPA (multivoxel pattern analysis) approach applied to MEG data (Tucciarelli et al., 2014) showed that the decoding of action intention (i.e., reaching, grasping) might occur earlier in the lateral OTC (200-600 ms) than in precentral regions (600-1200 ms). This result was consistent with the engagement of a posterior and ventral portion of the OTC found in response to typical (than atypical) object-related grasping actions (Valyear et al., 2010).

A modulation of the OTC response was found in clinical patients suffering from disorders related to body image. Individuals with a diagnosis of bulimia and anorexia nervosa exhibited reduced activity in the left OTC (Mohr et al., 2011) when observing images representing a distortion of their own body (i.e., fatter or thinner body). Specifically, the GM volume of the EBA in the left hemisphere was reduced in this population (Suchan et al., 2010), along with decrease effective connectivity between the FBA and EBA (Suchan et al., 2013) that was also negatively correlated with body size misjudgment. At the same time, Vocks and colleagues (2010a) showed that therapy focused on the reinforcement of body representation and awareness resulted in increased activity in the left EBA.

On the other hand, skilled experts showed a finest sensorimotor body representation (Jola et al., 2011) and proprioceptive abilities (Gautier et al., 2008). For intances, Jola and colleagues (2011) engaged dancers and non-dancers in a target location matching task, in which they had to reach a specific point on the below surface of a table using one of the two index fingers. The information about the location was presented visually, proprioceptively (with the other hand while blindfolded) or in a combination of the two modalities. Experts were more accurate than controls when have to rely only on proprioceptive information, and the contribution of this kind of information was greater in the multisensory condition. Reduced hand bias (target perceived as shifted and rotated) was also found in dancers suggesting a more coherent and less limb-specific representation of target hand position. Overall, these pieces of evidence are consistent with the modulation of our N2 component interpreted in light of visuomotor expertise with dance.

We were also interested in estimating the neural correlates of the N2 component. Therefore, two swLORETA source reconstructions were performed in the N2 time window in the group of experts and non-experts. The estimation of active dipoles in the brains of experts located the main neural sources in the FG (BA 37/20), MTG (BA 39/21) and precuneus/cuneus (BA 19) bilaterally (See Figure 3.12). Contrarily, the right cuneus (BA 19) was the strongest dipole identified in the brain of non-expert controls. Overall, this evidence seemed to confirm the hypothesis of reduced brain asymmetries as a result of acquired expertise.

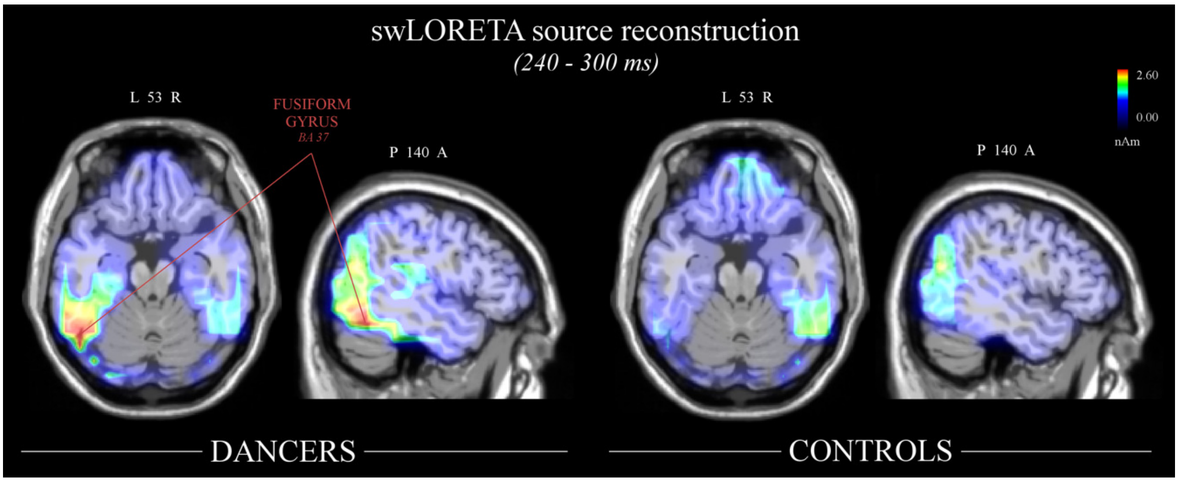


Figure 3.12. SwLORETA source reconstruction of surface potentials in the N2 time window (240-300 ms). SwLORETA performed on the grand-average waveforms (in the N2 time window 240-300 ms) in dancers (left side of the figure) and controls (right side of the figure). The axial and sagittal anatomical planes of the brain are shown. The activation of the left fusiform gyrus (BA 37) is visible only in the brains of dancers. The strongest magnitude values of the signal (nAm) are presented in red.

The activity in the visual regions was consistent with previous literature showing body- and face-selective areas within the inferior (FBA, FFA) and middle temporal (EBA) and occipito-temporal (OFA) regions (Cross et al., 2010; Peelen et al., 2005; Schwarzlose et al., 2005). The

N2 was measured at the same electrode sites often used for the N190 in response to the body, whose neural source was localized in the EBA (Ishizu et al., 2010; Taylor et al., 2007). Previously, increased experience with animals and object (McGuin et al., 2014; Wong et al., 2009) was linked to enhanced activity in the right OTC, while improved body awareness (Jola et al., 2011; Suchan et al., 2010) and face expertise (Tanaka et al., 2006) resulted in greater left OTC response. Furthermore, several visuomotor regions showed activity in the experts' group, including the IPL (BA 40), precentral (BA 6) and superior frontal (BA 9) gyri. Substantial number of studies shown the role of IPL (Chong et al., 2008; Orlandi et al., 2017), vPM (Iacoboni et al., 2005; Cross et al., 2006; 2009) and SFG (Calvo-Merino et al., 2005) in action perception, as part of the fronto-parietal mirror system (core regions of the AON). The activity in these regions was enhanced in response to known and trained movements when compared to novel movements, suggesting visuomotor simulation processes.

In the group of controls, the right anterior PFC (BA 10) showed to be strongly engaged during action observation, together with the precentral and postcentral gyri (BA 6, 3). Activity in the orbitofrontal cortex was found by Abreu and colleagues (2008) when non-experts made a good judgment of the action outcome. At the same time, experts showed activity in the insular cortex, suggesting different decision-making mechanisms depending on expertise level of the observer. A spatio-temporal shift from prefrontal to occipito-temporal regions was also found as a result of visual familiarity with objects (artificial faces) during a MEG categorization task (Kietzmann et al., 2016). This result suggested more efficient recognition processing of the repeated stimuli. Moreover, several evidences showed that a link between PFC engagement and perspective and working memory (Halahalli et al., 2015; Minamoto et al., 2015), in response to tasks that required the coordination of multiple cognitive processes (Benoit et al., 2011; Gilbert et al., 2006; Ramnani et al., 2004). Thus, in the present study, controls may have experienced increased cognitive effort/load to integrate body kinematic information into a defined complex action.

An expertise-related difference was also found in the posterior P2 response, as can be seen in Figure 3.6 and 3.7. The P2 component has been related to perceptual analysis of the stimulus, as shown by previous studies on face, object and implied motion perception (Boutsen et al., 2006; Freunberger et al., 2007; Li et al., 2016). The P2 latency has been interpreted as an index of the time required for perceptual processing, with less efficient coding characterized by slower peaks (Thorpe et al., 1996; Yang et al., 2012). Here we found an earlier P2 in the brains of the dancers (203 ms) compared with controls (218 ms), suggesting a faster and more effective encoding of dance kinematics. Contrarily, the controls not only showed a slower stimulus processing (later P2) but also required increased cortical resources, as indexed by the P2 amplitude modulation. The component was more positive over the posterior occipito-temporal sites (but not temporo-parietal sites) in non-dancers than dancers. This suggested enhanced activity of the body-related visual regions in non-expert observers. Increased P2 amplitude was previously reported during the observation of stimuli (i.e., faces) subsequently better remembered (Lucas et al., 2011), images depicting great motion content (Li et al., 2016), and during divided-attention tasks (Neumann et al., 2015). At the same time, a reduction of the P2 was found as a function of increasing expertise (Stahl et al., 2008).

In the present study, both the P2 and N2 components were faster over the right than left hemisphere, with the P2 being also larger over the right OTC. These results were consistent with previous evidence showing that, despite a bilateral engagement of OTC in body and motion perception (Hirai et al., 2005; Aleong et al., 2010; Vocks et al., 2010), the right hemisphere may have a prominent role (Downing et al., 2001; Cross et al., 2006). For instance, Aleong and Paus (2010) showed that the observation of body varying in size resulted in a larger activity in right OTC in female participants, while a bilateral response was found in the brains of male participants.

Finally, the fronto-central distributed P300 recorded over the midline sites showed to be sensitive to dance expertise, since it was larger in the brain of the dancers than controls (see Figure 7). This positivity was classically interpreted as indexing updating the mental representation of stimulus context, item recognition and categorization (Picton, 1992; Polich, 2007). EEG studies have shown a modulation of the component as a function of acquired expertise in high-skilled badminton players (Jin et al., 2011), dancers (Amoruso et al., 2014) and musicians (Proverbio et al., 2016). For instance, Jin and colleagues (2011) showed enhanced P300 over parietal sites in professional badminton players (compared with non-player controls) when asked to predict the ball's landing position during game action observation. Thus, we considered the enhanced P300 an indicator of refined gesture recognition in experts observers. At the same time, the reduced amplitude in controls suggested difficulty in action identification, that was likely the result of the lack of ballet expertise. This result was consistent with previous evidence showing enhanced ability to detect (Orlandi et al., 2017) and categorize action variations (Calvo-Merino et al., 2010) and violations (Proverbio et al., 2017) in professionals than control participants.

In conclusion, the observation of technical dance gestures elicited a posterior N2 component, that was modulated as a function of dance expertise. It was larger over the left hemisphere in the brains of dancers when compared with controls. The neural sources of the negativity were bilaterally distributed in experts, including inferior and middle temporal regions together with visuomotor cortices. In contrast, the visual and prefrontal areas in the right hemisphere were engaged in non-experts. Furthermore, the experts (relative to non-experts) showed an early P2 component followed by a larger P300, that suggested respectively as faster gesture processing (15 ms) and enhanced recognition. At the same time, the larger P2 over body-related regions in non-experts (compared with experts) indicated greater stimulus encoding, but weaker recognition ability (smaller P300). These pieces of evidence suggested refined tuning of the early OTC response to action kinematics as a result of intense and extensive whole-body training. Only the dancers exhibited more sophisticated and refined action processing within 300 ms after the occurrence of the gesture.

3.4. Effort coding in action observation

3.4.1. Data analysis

The mean area voltage of the frontal P300 component was measured at Fp1, Fp2, AFp3h, and AFp4h electrode sites during the 1050-1250 ms time window (see Figure 3.13). While, the mean area voltage of the parieto-occipital Late Positivity (LP) component was measured at P1, P2, POO3h, and POO4h electrode sites during the 1400-1600 ms time window. ERP data were subjected to multifactorial repeated measures ANOVA with one between-groups factor (group: experts, non-experts) and three within-groups factors, including effort (effortful, effortless), hemisphere (left, right), and electrode factors (2 levels depending on the ERP component of interest). Due to low signal-noise ratio, data from 4 participants (2 experts and 2 non-experts) have been discharged in these analyses. Brain activity from 15 experts and 15 non-experts was compared. Low-Resolution Electromagnetic Tomography (LORETA) was applied to the difference waves obtained by subtracting the ERPs for the effortless stimuli from those elicited by effortful stimuli between 1400-1600 ms in both groups of participants.

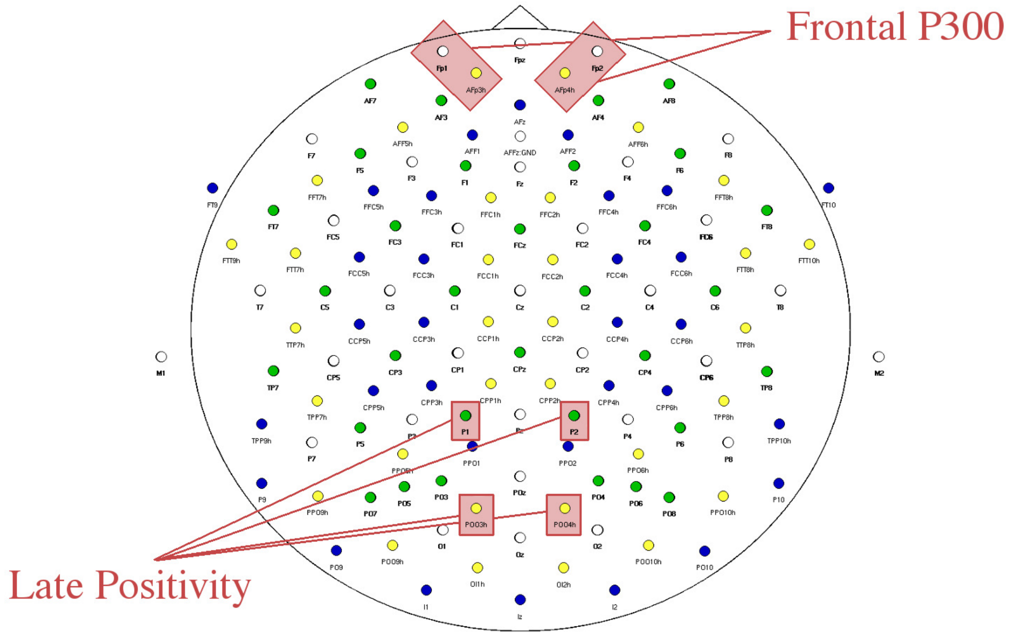


Figure 3.13. Schematic representation of the 128 electrode sites EEG-cap. The figure illustrates the position of the 128 electrodes on the scalp and those selected for the measurement of the three ERP components of interest.

3.4.2. Results

Frontal P300 (1050-1250 ms)

Repeated measure ANOVA performed on the amplitude values (μV) of the P300 showed a larger positivity in response to effortful (5.49 μV; SE = 0.47) than effortless (3.96 μV; SE = 0.34) movements, as indicated by the significant effort factor [F(1, 28) = 35.74, $p < 0.0001$].

The further effort X group interaction [F(1, 28) = 6.54, $p < 0.02$] and relative post-hoc comparisons showed that the effort-related difference in the P300 amplitude was significant only in experts (effortful: 6.33 μV; SE = 0.67; effortless: 4.13 μV; SE = 0.48; $p = 0.00017$) but not non-experts (effortful 4.66 μV; SE = 0.67; effortless: 3.78 μV; SE = 0.48; $p = 0.097$). This interaction can be appreciated in Figure 3.14 and Figure 3.15.

Finally, the statistical significant hemisphere factor [F(1, 28) = 5.77, $p < 0.03$] suggested that the P300 was more larger over the left (4.83 μV; SE = 0.40) than right (4.62 μV; SE = 0.38) hemisphere.

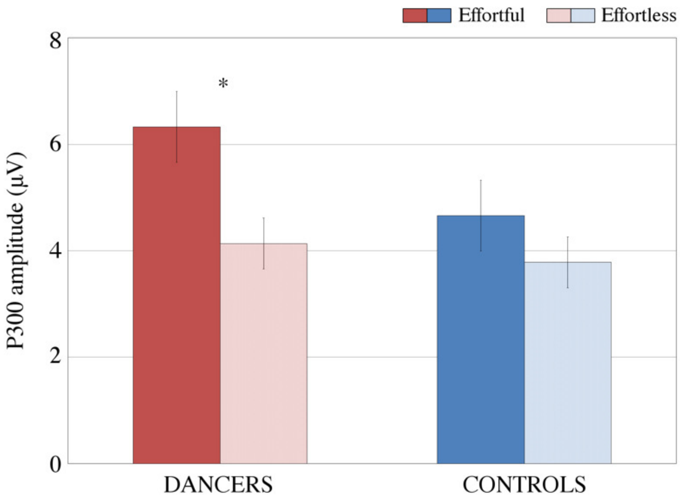


Figure 3.14. Amplitude values of P300 component. The histogram illustrates the mean amplitude values (µV) of the P300 recorded at frontal sites as a function of effort degree and group of participants. A greater positivity (P300) in response to effortful vs. effortless stimuli was found only in the dancers.

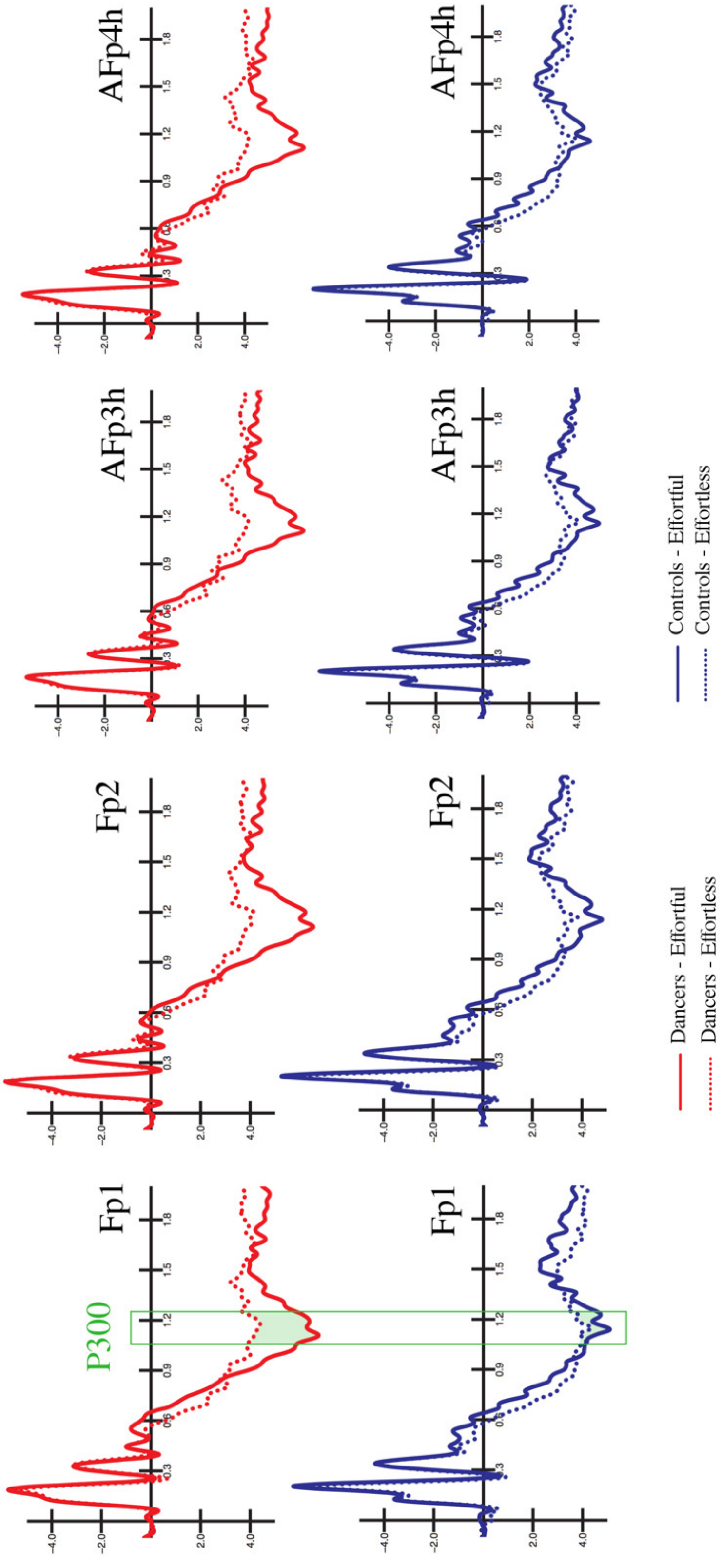


Figure 3.15. Figure 4. Grand average waveforms recorded at anterior sites. The figure illustrates the grand average waveforms (ERPs) recorded over frontal sites in the dancers (in the upper part of the image, in red) and controls (in the lower part of the image, in blue). The solid lines refer to the ERPs elicited by effortful movements, while the dotted lines refer to those elicited by effortless movements.

Late Positivity, LP (1400-1600 ms)

Repeated measure ANOVA performed on the amplitude values (μV) of the LP showed that the component was larger in response to effortful (2.41 μV; SE = 0.38) than effortless (1.70 μV; SE = 0.36) movements, as indicated by the significant effort factor [F(1, 28) = 15.92, $p < 0.001$].

The significant electrode factor [F(1, 28) = 49.45, $p < 0.0001$] showed a more positive component elicited over parietal (P1-P2:2.89 μV; SE = 0.36) than occipito-parietal (POO3h-POO4h:1.22 μV; SE = 0.40) sites.

The further triple effort X electrode X group interaction [F(1, 28) = 8.25, $p < 0.01$] showed that the effort-related modulation of the LP component was visible over both parietal (effortful: 2.96 μV; SE = 0.55; effortless: 1.95 μV; SE = 0.50; d = 0.50) and occipito-parietal (effortful: 1.08 μV; SE = 0.60; effortless: 0.17 μV; SE = 0.57; d = 0.40) sites in experts (p = 0.00014). Conversely, a significant difference was found over occipito-parietal sites (effortful: 2.20 μV; SE = 0.60; effortless: 1.46 μV; SE = 0.57; p = 0.00015) but not parietal sites (p = 0.64) in non-experts (see Figure 3.16 and Figure 3.17).

Finally, the LP elicited by effortful than effortless movements was larger over both left (effortful: 2.41 μV; SE = 0.40; effortless: 1.80 μV; SE = 0.38) and right (effortful: 2.42 μV; SE = 0.38; effortless: 1.60 μV; SE = 0.35) hemisphere (p = 0.00016), as indicated by the significant effort X hemisphere interaction [F(1, 28) = 4.83, $p < 0.04$]. Moreover, the LP in response to effortless stimuli was more positive over the left than right hemisphere (p = 0.032), while no hemispheric difference was found in response to effortful stimuli (p = 1).

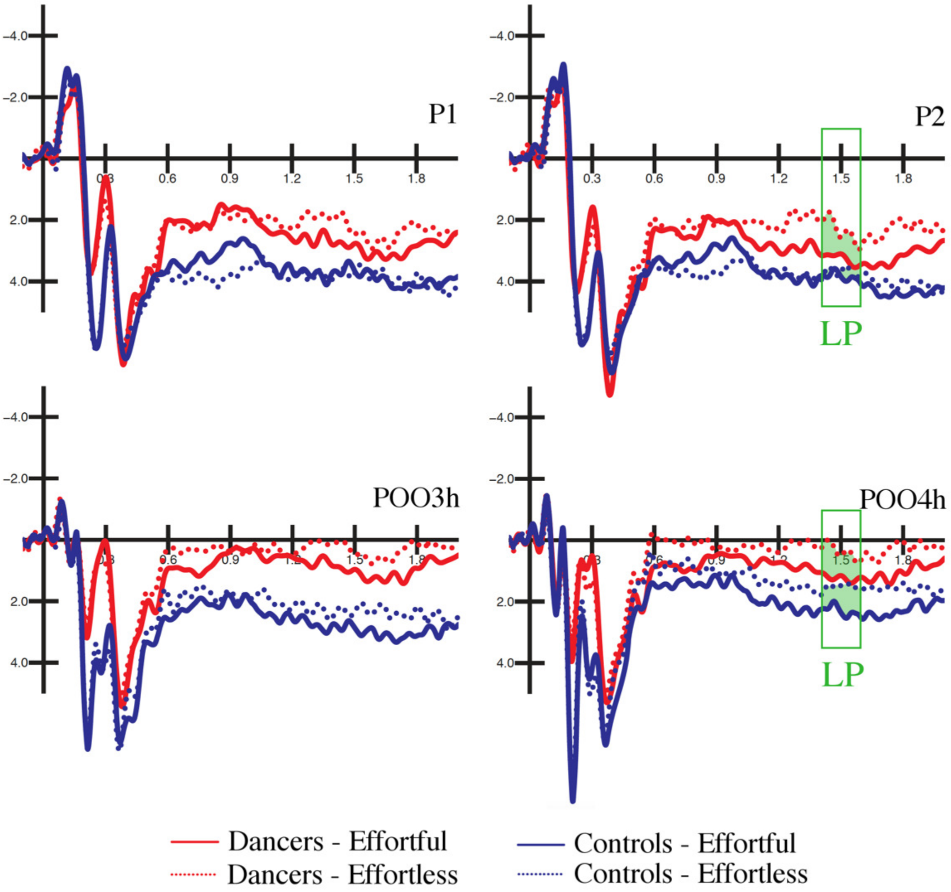


Figure 3.16. Grand average waveforms of LP component. The figure illustrates the grand average waveforms (ERPs) recorded over posterior sites of the scalp in the dancers (in red) and controls (in blue). The solid lines represent the ERPs elicited by effortful movements, while the dotted lines represent those elicited by effortless movements.

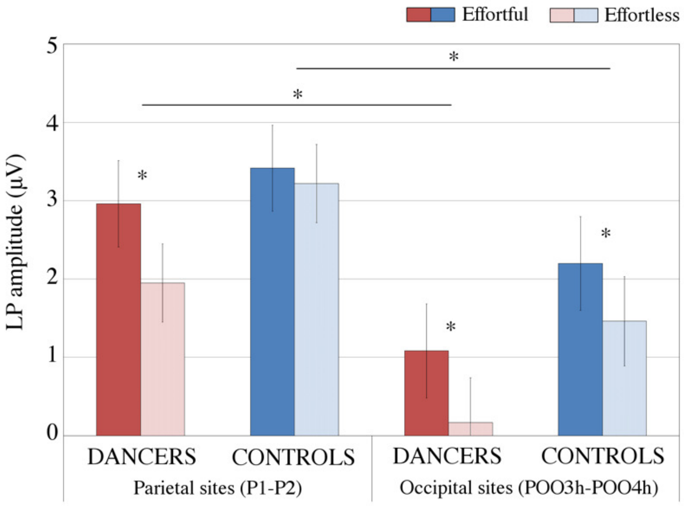


Figure 3.17. Amplitude values of LP component. The histogram illustrates the mean amplitude values (μV) of the LP recorded at parieto-occipital sites as a function of effort, electrode and group factors. A greater positivity (LP) in response to effortful vs. effortless stimuli was found in all participants over occipital sites (POO3h-POO4h), whilst only in dancers was also shown over parietal sites (P1-P2).

swLORETA source reconstruction (1400-1600 ms)

Two swLORETA source reconstruction were performed (one for each group of participants) on the difference wave obtained by subtracting the ERPs for effortless from those elicited by effortful stimuli, in the LP time window (1400-1600 ms). The main active dipoles included the superior temporal gyrus/uncus bilaterally (BA 38) and the fronto-parietal system (BA 40, 6/8) in the brains of experts (see Table 3.4). Conversely, task-related frontal regions (BA 10), body- and motion-related visual regions (BA 19, 20, 37) were identified as more active in non-experts (see Table 3.5).

DANCERS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
7.09	-48.5	8.2	-20	L	T	STG	38	Multisensory Integration
4.82	21.2	9.1	-27.5	R	T	Uncus/STG	38	
5.81	60.6	-40.6	34	R	P	Supram Gyrus	40	Fronto-parietal system
2.96	-58.5	-31.4	43.8	L	P	IPL	40	
4.19	-18.5	30.5	49.8	L	F	SFG	8/6	
6.64	-58.5	-9.4	-14	L	T	ITG	21	Body and notion related visual regions
4.52	11.3	-69	13.6	R	O	Cuneus/PCC	18/31	
4.52	1.5	-73	49.2	R	P	Precuneus	7	
3.56	40.9	55.3	7	R	F	MFG	10	Task related

Table 3.4. Active electromagnetic dipoles list. List of active electromagnetic dipoles identified in dancers according to swLORETA in the Late Positivity time windows (1400-1600 ms), with the relative Talairach coordinates. The strongest sources of activation included the superior temporal gyrus, fronto-parietal system and few visual areas devoted to face, body, and motion processing in the dancers. (Legend: Magn - magnitude, Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann Area)

CONTROLS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
12.4	-38.5	46.3	-2.3	L	F	IFG	10	Task related
9.46	-8.5	65.3	7.9	L	F	SFG	10	
8.96	1.5	57.3	-9	R	F	MedFG	10	
7.07	21.2	55.3	7	R	F	SFG	10	
6.93	31	53.4	24.8	R	F	SFG	10	
5.89	31	9.1	-27.5	R	T	STG	38	Multisensory integration
4.78	21.2	-68	4.7	R	O	Lingual Gyrus	19	Body and motion related visual regions
5.56	50.8	-0.6	-28.2	R	T	MTG	21	
5.17	-48.5	-67.1	-3.5	L	O	MOG	37	
4.89	21.2	-66.1	-10.9	R	O	FG	19	
4.77	11.3	-70	22.5	R	P	Precuneus	31	
4.44	50.8	-33.7	-23.6	R	T	FG	20	
3.82	60.6	-56.9	-2.8	R	T	MTG	21	
3.72	50.8	0.4	47.2	R	F	Prec Gyrus	6	Fronto-parietal system
2.57	50.8	-32.4	52.7	R	P	IPL	40	

Table 3.5. Active electromagnetic dipoles list. List of active electromagnetic dipoles identified in controls according to swLORETA in the Late Positivity time windows (1400-1600 ms), with the relative Talairach coordinates. The main dipoles in controls were instead located in the rostral prefrontal cortex (BA 10), and in face-, body- and motion-related visual regions. (Legend: Magn - magnitude, Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann Area)

3.4.3. Discussion

The second aim of the present study was to investigate the encoding of muscular effort during action observation as a function of dance expertise. Several pieces of evidence showed that the observation of effortful than effortless actions (i.e., running vs. walking) resulted in increased autonomic responses, including heart and breath rate. Larger ERP late potentials were recorded in response to images depicting dynamic vs. static gesture (Proverbio et al., 2009). Moreover, enhanced muscle-specific and time-dependent corticospinal excitability was found in TMS studies during the observation of heavy vs. light object lifting (Alaerts et al., 2010a; 2010b). Despite this evidence suggesting an engagement of visuomotor simulation processes in action understanding, other authors proposed a role of the mentalizing system (TPJ) in effort coding (Mizuguchi et al., 2016). Here, we compared the bioelectrical activity of the brain of ballet experts and non-experts in response to complex technical gesture varying in the amount of muscular effort required. We hypothesized to find a strong impact of dance training on action representation, with professional dancers (than controls) showing a more refined and automatized encoding of effort information, due to acquired motor knowledge.

Two main ERP components showed to be effort-sensitive in separate time windows as a function of acquired expertise with ballet. A first positivity was recorded between 1050 and 1250 ms (P300) over frontal sites, while a second positivity raised between 1400 and 1600 ms (Late Positivity, LP) over centro-parietal sites. The P300 component reached the maximum peak at approximately 1140 ms, concurrent with the video frame representing the effort culmination (i.e., maximal height or spread of the limbs during a jump) in each clip (at 1000 ms). Furthermore, effortful steps when compared with effortless steps elicited a larger P300 in the brains of the dancers but not controls. Namely, the frontal positivity was not modulated by the effort condition in non-dancers. According to the scalp distribution and latency, the P300 was interpreted as an index of encoding processes of the movement. The potential was named this way as part of the family of the endogenous positive components associated with the updating of the mental representation prompted by the incoming stimulus (Polich, 2007), and to distinguish it from the following LP.

Previous studies have shown a relationship between increased anterior positive components during stimuli observation and greater accuracy in subsequent memory recalling. One example is the EEG study by Koenig and colleagues (2008), in which the volunteers were shown pictures characterized by different valence (positive, negative and neutral) and arousal during a memory task. They were instructed to memorize the stimuli to attend a subsequent recall phase in which they were engaged in both old/new and source decision task. The results showed that the low-arousal positive (than negative and neutral) images were remembered more efficiently and gave rise to larger anterior slow waves. The amplitude of this component was also enhanced in response to remembered than forgotten stimuli, suggesting increased encoding processes during observation. In another study (Mangels et al., 2001), a positive, sustained potential was found over prefrontal and posterior sites of the scalp (between 1000 and 1500 ms) during the encoding of lists of words that would have been subsequently recalled and remembered (than non-remembered). In this time windows, the anterior component was also larger on the left than right hemisphere during focus attention than divided attention (secondary pitch detection task). This left asymmetry was consistent with the P300 distribution in our study, that was more positive over the left frontal regions regardless of the expertise level.

This result is also in accordance with the HERA (hemispheric encoding/retrieval asymmetry) model of memory proposed by Tulving (Nyberg et al., 1996) and revised by Habib and colleagues (2003). A prominent role of the left PFC would be played during memory encoding of a stimulus, while the PFC in the right hemisphere would be more involved in following memory retrieval. In this regard, an EEG study by Babiloni and colleagues (2006) showed evidence in favor of the HERA model prediction. The authors engaged the participants in a memory task with images of places (i.e., interiors, landscapes). In the encoding phase, the volunteers were instructed to categorize the stimuli, while in the retrieval phase they were asked to recognize the previously presented stimuli. Enhance coherence in the gamma frequency band (40 Hz) was found between fronto-parietal sites in the left hemisphere during the encoding phase of the stimuli. A similar effect was shown in the right hemisphere during the subsequent retrieval phase. Moreover, a bidirectional pattern of information flow between fronto-parietal sites (estimated by the direct transfer function, DTF) was specifically found in the left hemisphere during encoding and in the right hemisphere during retrieval. This result showed a parallel and opposite flow of information between frontal and parietal regions, as hypotetized by the HERA model. More recently, Friese and colleagues (2013) showed increased activity in the theta and gamma frequency band in response to remembered than forgotten stimuli respectively at frontal and parietal sites. A phase-amplitude coupling between theta and gamma oscillation was also found, being larger for subsequently remembered pictures. Frontal midline theta oscillations were previously linked to episodic encoding/retrieval and working memory maintenance (for a review see Hsieh and Ranganath, 2014). Overall, this evidence seemed to suggest that increased amplitude of the frontal positivity may be the result of refined encoding of action information in experts. Given that our stimuli differed only in the level of effort represented, we speculated a greater ability to encode effort information (action kinematics) in individuals who have previously acquired the specific motor knowledge with the observed actions.

A second component over posterior sites showed to be sensitive to effort information as a function of ballet expertise. Specifically, a larger positivity (LP) in response to effortful than effortless gesture was found in the brains of dancer participants over parietal and occipital regions. In contrast, non-dancer controls showed a modulation of the LP only over occipital sites. The different distribution on the scalp suggested the engagement of different cognitive processes. Whether increased effort resulted in enhanced activity in the visual regions in all participants, visuomotor resonance processes likely occurred only in the brains of experts. The late positivity is an ERP component usually interpreted as an index of high-order cognition and information integration and showed to by modulated the content of the stimulus. Several studies have shown that emotional and arousing stimuli gave rise to larger LP amplitude when compared with neutral stimuli (Bayer and Schacht, 2014; Codispoti et al., 2007; Schupp et al., 2000). Also, selective visual attention toward a specific part of the stimulus can increase the positivity of the component (Hajcak et al., 2009; 2013). Previously, Proverbio and colleagues (2009) found enhanced LP during the observation of images representing dynamic/effortful than static/effortless human action. The authors interpreted the results as an increased processing of kinematic information conveyed by the effortful stimuli.

Similarly, in the present study, the LP distribution over the occipital visual regions may be the result of increased amount of motion and body information conveyed by the effortful steps. The more parietal distributed LP found in the experts also suggested the engagement of visuomotor areas due to acquired expertise. This interpretation was supported by previous evidence that showed event-related desynchronization (ERD) over sensorimotor regions of individuals engaged in action observation. Decreased power in the mu (μ) frequency band (8-12 Hz) was found over centro-parietal sites during action processing. (Coll et al., 2017; Yin et al., 2016). The most accepted interpretation of this suppression effect is the relationship with the activity of the fronto-parietal mirror system (Fox et al., 2016; Hobson et al., 2017), that allows a motor simulation of the observed action. It is well-known that the activity of this network can be modulated by acquired expertise during the action observation (Orgs et al., 2008), outcome prediction (Denis et al., 2017) and error detection (Babiloni et al., 2010), as shown by desynchronization in the mu/alpha and beta frequency band. More important, Quandt and Marshall (2014) found changes in the alpha (8-10 Hz) spectrum during the observation of simple effortful vs. effortless action. The participants attended interaction (brief or extended) with objects varying in weight or just received information (semantic knowledge) about the characteristics of the stimuli. After both types of training, the observation of heavy object lifting led to stronger ERD rather than light object-related actions. This effect was absent in individuals who were only informed about the two categories of objects. Thus, acquired experience showed a role in modulating the sensitivity in predicting sensorimotor consequences of the action.

To further investigate the role of expertise in modulating the encoding of effort information, the neural sources of the LP component were estimated by swLORETA. The LP showed to be sensitive to the effort manipulation (differently) in both groups of participants, contrarily to the P300 response. swLORETA source reconstruction was performed on the difference wave (effortful-*minus*-effortless) in experts and non-experts (see Figure 3.18). In the group of professionals, the main active dipoles were located in the STG (BA 38), IPL (BA 40) bilaterally, left precentral gyrus (BA 6/8) and a few body- and motion-related visual regions (BA 21, 18, 7). In the control group, they were located in task-related frontal areas (BA 10) bilaterally and in several visual (BA 19, 20, 21, 31, 37) and mirror (BA 6, 40) regions in the right hemisphere.

The STG/STS in an associative area with multiple connections with cortical and subcortical structures, including the OFC, amygdala, and cerebellum (Erickson et al., 2017; Mier et al., 2014; Sokolov et al., 2012). Thus, its role in several processes has been shown, including multisensory integration and socioemotional processing (Olson et al., 2007). While the anterior temporal lobe has a role as amodal semantic hub, the posterior part of STS is engaged in biological motion perception, imitation and outcome prediction (Herrington et al., 2011; Molenberghs et al., 2010; Thompson et al., 2005), providing input to the fronto-parietal system (Rizzolati and Craighiero, 2004). Modulation of the structure (thickness) and activity of this region was previously shown (Karpati et al., 2017; Orlandi et al., 2017), together with a specific engagement of the left STG, PM and right IPC as a function of expertise (Kirsch and Cross, 2015). Contrarily to the study by Mizuguchi and colleagues (2016) in which activity was found in the STS and TPJ, we also identify the IPL and PM as active dipoles (Pau et al., 2013). The IPL is usually engaged in action observation, preparation and imagination (Arnstein et al., 2011; Buccino et al., 2001; 2004; Chong et al., 2008), especially when the movement stimulus is well-known to the observer (Cross et al., 2006; 2009; Gardner et al., 2015). The engagement of promotor regions is consistent with TMS studies that showed enhanced corticospinal excitability in response to heavy than light action lifting (Alaerts al., 2010a; 2010b; Zénon et al., 2015).

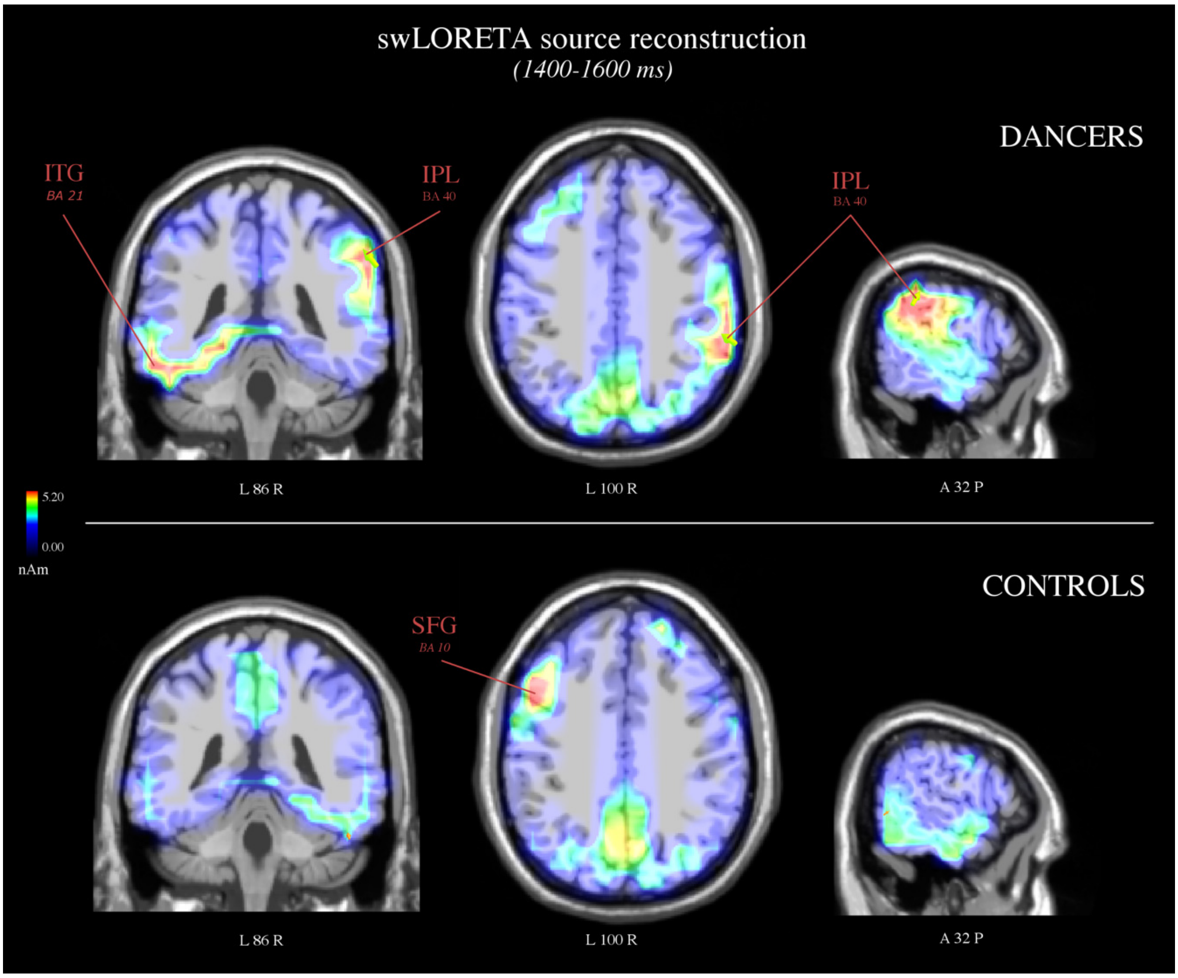


Figure 3.18. SwLORETA source reconstruction of surface potentials in the LP time window (1400-1600 ms). SwLORETA performed on the *difference wave* obtained by subtracting the ERPs elicited by effortless stimuli from those elicited by effortful stimuli (in the LP time window 1400-1600 ms) in dancers (upper part of the image) and controls (lower part of the image). The coronal, axial and sagittal anatomical planes of the brain are shown. The activation of the right inferior parietal lobule (IPL, BA 40) and the left inferior temporal gyrus (ITG, BA 21) is visible in the brain of dancers. The activation of the left superior frontal gyrus (SFG, BA 10) in the brain of the controls can also be appreciated. The strongest magnitude values of the signal (nAm) are shown in red.

At the same time, the relevant activation of the anterior or rostral PFC (BA 10) in non-experts, suggested higher cognitive effort/load in dance kinematics encoding. The aPFC has been previously linked to working memory, encoding and maintenance of new information, along with prospective memory (Benoit et al., 2011; Gilber et al., 2006). For example, increased aPFC activity was observed when a secondary task was overlapped to the main one (Minamoto et al., 2015; Momennejad et al., 2013) or incremental updating of working memory was required (Halahalli et al., 2015). In our study, greater activity within the OTC was found in controls than dancers, suggesting increased processing of body kinematics and motion detail in individuals without a motor knowledge of the effortful steps. Overall, dance expertise was associated with a more bilateral distributed active brain network. This evidence was consistent with previous results found in expert musicians (Moore et al., 2014; Rüber et al., 2015). Musical practice leads to visuomotor and auditory skills acquisition, including the bimanual coordination, notes to movement translation, and refined auditory processing. Different authors showed enhanced functional symmetry in musicians (than controls) during music listening (Burunat et al., 2015) and score reading (Proverbio et al., 2013). Enhanced interhemispheric connectivity has also been found, as indexed by structural and functional changes in the corpus callosum of experts (Steele et al., 2013). Similarly, the neuroplastic changes that possibly occurred after extended and intense dance practice (Giacosa et al., 2016; Hänggi et al., 2010; Hüfner et al., 2011) might partially explain the increased symmetry in brain response to action observation found in this investigation.

In conclusion, the results from the present study suggest more automatic and refined processing of effort information during the encoding of gesture in trained participants. The expert showed a modulation of the frontal (P300) and parietal positivity (LP) as a function of increased muscular effort depicted by the action. The reconstruction of the source of the LP component identified fronto-parietal mirror (PM and IPL) and associative temporal (STG) regions in effort encoding in the dancers. Thus, the motor knowledge acquired during years of practice, allowed the professional to encode effort information automatically and more efficiently during action observation. Contrarily, the modulation of the LP over occipital sites in controls and the relative engagement of working memory (aPFC) and OTC regions possibly indicates greater cognitive load in codifying and integrate body information in a consistent movement.

3.5. Motor imagery of dance action

3.5.1. *Data analysis*

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 (see Figure 3.19). The post-hoc comparisons were computed using Duncan's test. Overall, the ERP data were subjected to multifactorial repeated measures ANOVA with one between-groups factor (group: experts, non-experts) and three within-groups factors, including effort (effortful, effortless), hemisphere (left, right), and electrode factors (AFF, F, FFCh). Due to low signal-noise ratio, data from 2 participants (1 expert and 1 non-expert) were eliminated from these analyses. Brain activity from 16 experts and 16 non-experts was compared. Low-Resolution Electromagnetic Tomography (LORETA) was applied to the difference waves obtained by subtracting the ERPs for the effortless stimuli from those elicited by effortful stimuli between 400-550 ms in both groups of participants.

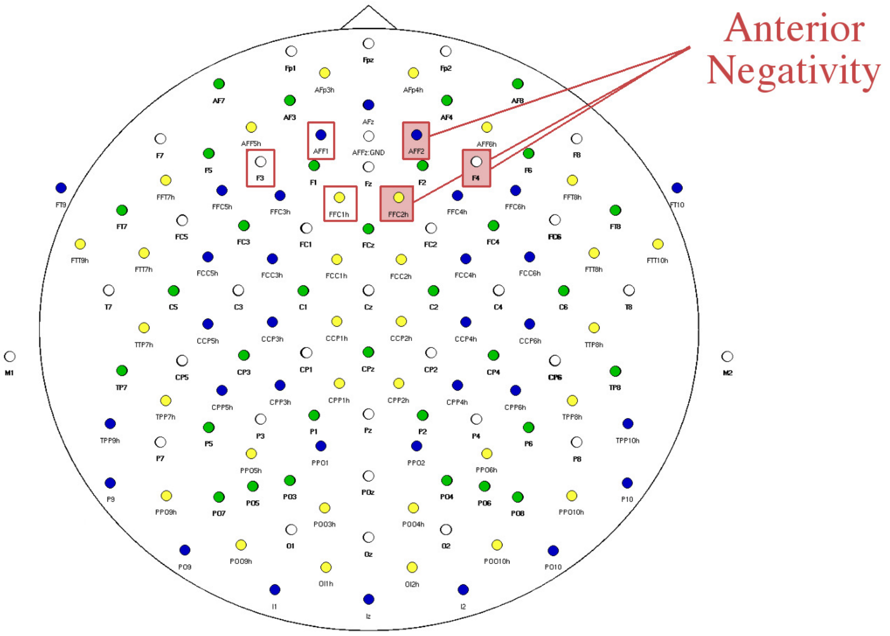


Figure 3.19. Schematic representation of the 128 electrode sites EEG-cap. The figure illustrates the position of the 128 electrodes on the scalp and those selected for the measurement of ERP component of interest.

3.5.2. Results

Anterior Negativity, AN (400-550 ms)

Repeated measure ANOVA performed on the amplitude values (μV) of the AN component showed that the negativity was larger in the experts (-2.11 μV, SD = 0.28) than non-experts (-1.05 μV, SD = 0.28), as suggested by the significant group factor [F(1, 30) = 7.018, $p < 0.02$]. Figure 3.23 illustrates the grand average waveforms (ERPs) recorded over all 128 sites of the scalp as a function of the group.

The further group X effort interaction [F(1, 30) = 11.703, $p < 0.003$] and relative post-hoc comparisons showed that the AN component in response to effortless movements (p = 0.002) was larger in experts (-2.37 μV, SD = 0.28) than non-experts (-0.83 μV, SD = 0.28). No group difference in effortful-related ERP was found (p = 0.18). The AN was more negative in response to effortful (-1.27 μV, SD = 0.32) than effortless (-0.83 μV, SD = 0.28) movements in non-experts (p = 0.04). However, the opposite effect was found in the brain of experts (p = 0.01), which showed a larger negativity in response to effortless (-2.37 μV, SD = 0.28) than effortful (-1.85 μV, SD = 0.32) movements (see Figure 3.20 and Figure 3.21).

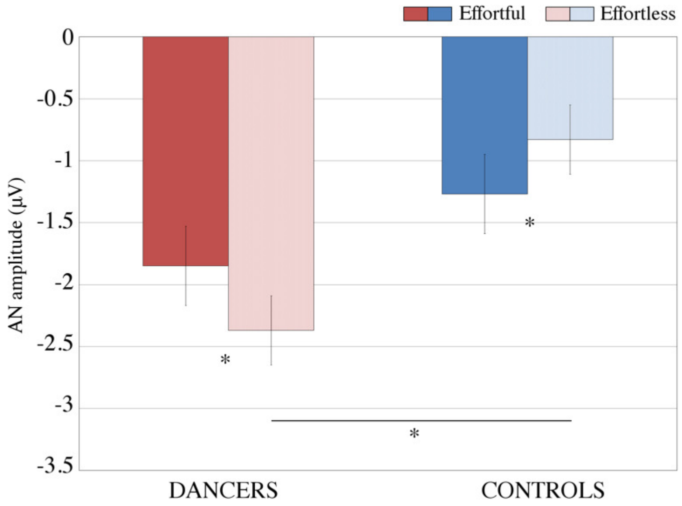


Figure 3.20. Amplitude values of AN component. The histogram illustrates the mean amplitude values (μV) of the AN recorded at anterior sites as a function of effort degree and group of participants. A greater negativity in response to effortful vs. effortless stimuli was found in the controls. At the same time, effortless vs. effortful steps elicited an enhanced AN in the dancers.

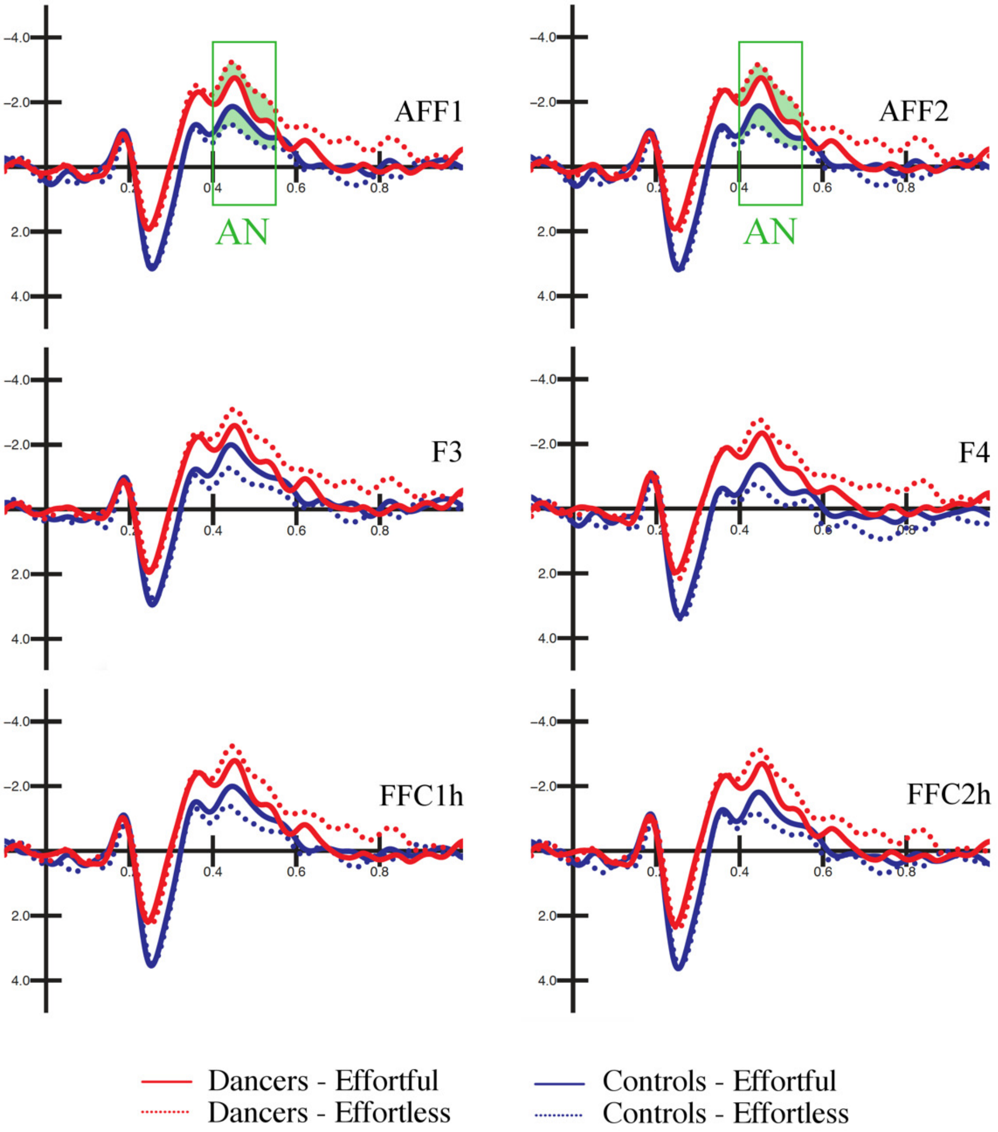


Figure 3.21. Grand average waveforms of AN component. The figure illustrates the grand average waveforms (ERPs) recorded over anterior sites of the scalp in the dancers (in red) and controls (in blue). The solid lines represent the ERPs elicited by effortful movements, while the dotted lines represent those elicited by effortless movements.

In addition, the AN was more negative over the left (-1.67 μV, SD = 0.21) than right (-1.49 μV, SD = 0.19) hemisphere [F(1, 30) = 77.108, $p < 0.001$].

The significant electrode factor [F(2, 60) = 9.288, $p < 0.001$] indicated a larger AN over the medial (Aff1-Aff2: -1.64 μV, SD = 0.21; FFC1h-FFC2h: -1.65 μV, SD = 0.21) than lateral (F3-F4: -1.45 μV, SD = 0.19) sites of the scalp.

Lastly, the electrode X hemisphere interaction [F(2, 60) = 5.485, *p* < 0.007] and relative post-doc tests showed that the AN was more negative over the left than 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). Moreover, the difference between medial and lateral sites previous reported was significant only over the right (*p* < 0.001) but not left (*p* = 0.94) hemisphere (see Figure 3.22).

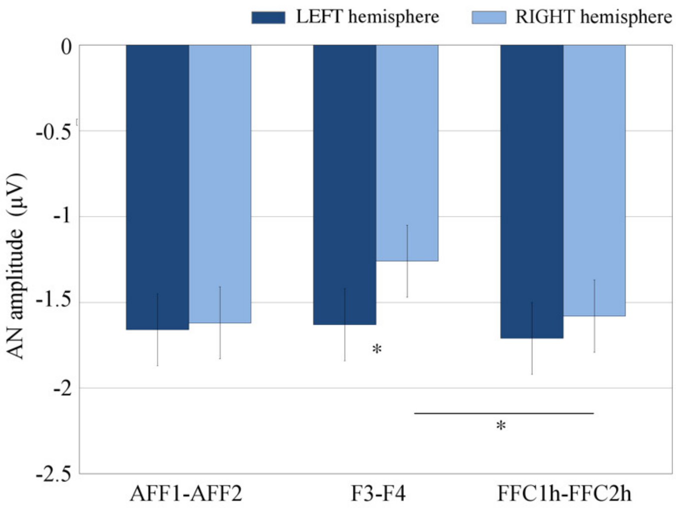


Figure 3.22. Amplitude values of AN component. The histogram illustrates the mean amplitude values (μV) of the AN recorded at anterior sites as a function of electrode site and hemisphere factors. A greater negativity was found in the left vs. right hemisphere at lateral electrode sites.

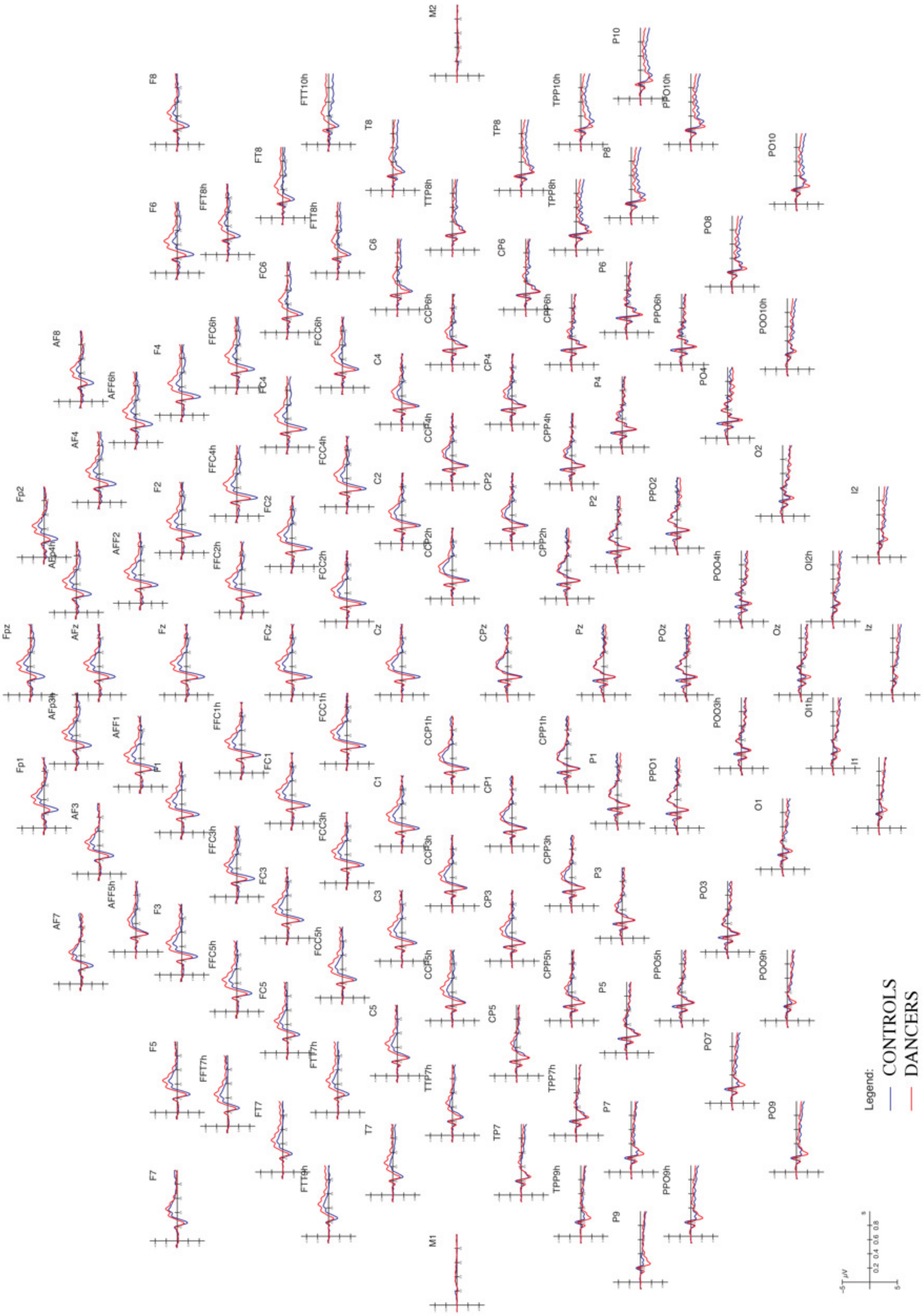


Figure 3.23. Grand average waveforms recorded from all 128 electrode sites. The figure illustrates the grand average waveforms (ERPs) recorded over all 128 sites of the scalp in the dancers (in red) and controls (in blue).

swLORETA source reconstruction (400-550 ms)

Two swLORETA source reconstruction was performed on the difference wave obtained subtracting the ERP in response to effortless movements from those in response to effortful movements, one for each group of participants. The swLORETA was applied on the same time window of the AN (400-550 ms). The main dipoles were located in the body-, face- and motion-related visual regions (BA 37, 20/21, 18/19) in the brains of experts (see Table 3.6), while the task-related frontal regions (BA 10, 11) showed the larger magnitude in non-experts (see Table 3.7). Temporal associative areas (BA 38, 28) were also active in both groups. Finally, greater engagement of fronto-parietal mirror regions (BA 40, 6, 9) was found in experts than non-experts.

DANCERS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
4.88	50.8	-33.7	-23.6	R	T	FG	20	Body, face and motion related visual regions
4.46	50.8	-16.1	-22.2	R	T	FG	20	
2.88	-58.5	-55	-17.6	L	T	FG	37	
2.70	-8.5	-99.4	11	L	O	Cuneus	18	
2.69	40.9	-75.2	-19.1	R	O	FG	19	
4.40	50.8	-0.6	-28.2	R	T	MTG	21	Associative
4.29	31	9.1	-27.5	R	T	STG	38	
3.79	-8.5	-0.6	-28.2	L	Lim	Uncus	28	
3.64	-58.5	-1.4	-20.8	L	T	MTG	21	
2.33	-28.5	55.3	7	L	F	MFG	10	Task related
2.25	1.5	-20.3	26.8	R	Lim	CG	23	
2.17	-18.5	-1.1	65	L	F	SFG	6	Fronto-parietal system
2.15	-58.5	-6.3	37.4	L	F	Prec Gyrus	6	
1.94	21.2	52.4	33.7	R	F	SFG	9	
1.78	40.9	-30.4	34.9	R	P	IPL	40	
1.77	60.6	-30.4	34.9	R	P	IPL	40	
1.74	1.5	-43.5	60.7	R	F	Parac Gyrus	5	
1.72	-28.5	-33.4	61.6	L	P	Postc Gyrus	3	

Table 3.6. Active electromagnetic dipoles list. List of active electromagnetic dipoles identified in dancers according to swLORETA in the Anterior Negativity time windows (400-550 ms), with the relative Talairach coordinates. The main dipoles in controls were located in face-, body- and motion-related visual regions, associative areas and fronto-parietal regions. (Legend: Magn - magnitude, Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann Area)

CONTROLS

Magnitude	*T-x [mm]*	*T-y [mm]*	*T-z [mm]*	*Hem*	*Lobe*	*Gyrus*	*BA*	*Function*
4.73	11.3	64.4	16.8	R	F	SFG	10	Task related
4.21	1.5	57.3	-9	R	F	MEDFG	10	
3.65	-28.5	37.2	-10.5	L	F	MFG	11	
4.11	40.9	18.2	-19.3	R	T	STG	38	Associative
4.07	50.8	-0.6	-28.2	R	T	MTG	21	
3.34	-18.5	9.1	-27.5	L	T	STG	38	
2.97	60.6	-55	-17.6	R	O	FG	37	Body, face and motion related visual regions
2.49	-8.5	-90.3	20.8	L	O	Cuneus	18	
2.40	-48.5	-65.1	-18.4	L	O	FG	37	
2.27	31	-88.3	3	R	O	MOG	18	
2.33	-38.5	21.4	40	L	F	Prec Gyrus	9	Fronto-parietal system
2.27	-18.5	-73	49.2	L	P	Crecuneus	7	
2.04	40.9	-7.8	55.2	R	F	Prec Gyrus	6	
1.87	60.6	-41.5	42.9	R	P	IPL	40	

Table 3.7. Active electromagnetic dipoles list. List of active electromagnetic dipoles identified in controls according to swLORETA in the Anterior Negativity time windows (400-550 ms), with the relative Talairach coordinates. The main dipoles in controls were instead located in the rostral prefrontal cortex (BA 10), associative regions (BA 38) and in face-, body- and motion-related visual regions. (Legend: Magn - magnitude, Hem - hemisphere, T - temporal lobe, P - parietal lobe, F - frontal lobe, O - occipital lobe, BA - Brodmann Area)

3.5.3. Discussion

Previous evidence has shown that the mental simulation of a movement from the first-person perspective leads to engagement of dorsal fronto-parietal regions of the brain, including premotor and parietal cortices (Ptak et al., 2017). Increased muscle-specific corticospinal excitability (Fourkas et al., 2008) was reported during the kinaesthetic motor imagery (MI) along with modulation of the alpha, beta, and theta band rhythms (Yi et al., 2013). Moreover, action complexity, body parts involved, and repertoire familiarity resulted in different recruiting of brain regions during MI (Olsson and Nyberg, 2010). In this regard, the third aim of the present study was to investigate the impact of dance expertise on the MI of technical gesture varying in the required effort.

As can be appreciated in Figure 3.23, the imagination of dance action elicited a negative component that reached the maximum amplitude over anterior sites of the scalp. This Anterior Negativity (AN) potential (400-550 ms) was larger in experts than non-expert controls. Thus, it was interpreted as an index of increased neural processing by frontal regions as a function of acquired expertise. Previously, Cebolla and colleagues (2015) showed that imaging to throw a tennis ball in a virtual tennis court (compared to rest) resulted in long-lasting negativity over fronto-central sites with two peaks at approximately 300 (N300) and 1000 ms (N1000). Enhanced theta (4-7 Hz) frequency band amplitude over frontal midline was also found in another EEG study during MI of dart throwing after kinaesthetic motor training (Weber et al., 2016). This modulation was also associated with an increased performance level. A before/after training difference was specifically visible 1000 ms before the volunteers imagined releasing the dart (cued by button press). This result was interpreted as better allocation of attentional resources during motor imagery after kinaesthetic MI practice.

Another evidence on expertise-related modulation of MI processes was provided by the TMS study by Fourkas and colleagues (2008). The authors showed enhanced corticospinal excitability during MI of practiced tool-related movements rather than kinematically similar non-practiced movements. The larger MEPs obtained from the hand muscles were interpreted as an index of more sophisticated cortical representation of specific hand actions in experts, recalled during MI. Moreover, fMRI evidence showed greater activity in frontal regions during repertoire specific MI in experts than non-experts. A case in point was the study by Chang and colleagues (2010), by which activity in the SMA of elite archers was found during MI of archery shooting. Broader engagements of brain regions were identified in non-archers, including SMA, pre-SMA, IPC, IFG. Activity was also shown in the cerebellum and basal ganglia (BG) of non-experts likely associated with motor learning of the un-trained shooting. Contrarily, archers exhibited a more organized and efficient brain network for motor planning that integrates visual and motor information. These results corroborate previous findings of BG and limbic recruitment (i.e., posterior cingulate cortex) found in non-expert golf players during MI of golf puff, while skilled players exhibited engagement of dorsolateral PM, SPL and occipital regions (Milton et al., 2007). Finally, enhance activity in the prefrontal regions was shown in experts (than non-expert) divers during MI of technical actions (diving and gymnastics), indexing the importance of motor and sensory information for skilled athletes. A specific activity also emerged in the parahippocampal gyrus in divers but not controls, when directly comparing MI for diving vs. gymnastics movements (Wei and Luo, 2010).

In the present study, despite being larger over the middle than lateral electrode sites, the AN was more negative over the left than right hemisphere at lateral sites. This evidence was consistent with previous findings showing left hemispheric dominance for MI (Olsson et al., 2008) and motor planning (Kuhtz-Buschbeck et al., 2003) in addition to fine motor control processes (Serrien et al., 2006). For instance, in a study by Kuhtz-Buschbeck and colleagues (2003), the participants were instructed to execute or imagine simple (compression of an object with two fingers) and complex (sequence of finger-to-thumb opposition) movements using the right and left hand. MI of simple movements with both hands engaged overlapping brain regions including the left dorsal PM, frontal operculum, and SMA. Left ventral PM, cerebellum, and intraparietal regions were also active during MI of complex action. Enhanced activity in the left MFG was shown during imagery when directly compared with real execution. In a further TMS study by Stinear and colleagues (2006), the volunteers were performing a thumb-to-finger MI task using the left, right or both hands together, while a TMS pulse was delivered over M1 on both hemispheres . Modulation of the MEP was found when the pulse was delivered over the left MI, concurrently with the EMG burst recorded during the real execution of the action. This effect was visible for MI with unimanual and bimanual actions. Contrarily, no modulation was found after stimulation of the right M1. These findings suggested muscle- and time-specific facilitation as well as a prominent role of the left hemisphere in motor imagery. Clinical studies involving patients with stroke (Sabaté et al.., 2004; Yan et al., 2012) confirmed the importance of the left hemisphere in MI. For instance, reduced velocity during real and imagined execution of finger movements (dorsal extension-ventral flexion) using both hands was shown in an individual with left-brain damage (parietal motor cortex and internal capsule). Contrarily, a damage on the right hemisphere affected only the contralateral hand movements (Sabaté et al., 2004).

More importantly, in the present study, the motor content of the stimuli affected the amplitude of the AN in an expertise-specific manner. Effortful steps elicited greater negativity in the brain of controls but not dancers. The experts exhibited an opposite pattern of results, showing increased AN during the imagination of effortless than effortful movements. Previous studies have shown modulation of MI processes as a function of body parts involved or action complexity. At our actual knowledge, no previous evidence identified similar opposite effects of motor content when comparing experts and non-experts. In this regard, TMS studies have shown enhanced corticospinal excitability when participants imagined executing finger (Helm et al., 2015) and foot (Kato et al., 2017) movements that differed concerning force requirements. Also, Szameitat and colleagues (2007) showed engagement of different brain regions when directly comparing MI of movement executed with upper limbs and whole-body. The medial and superior lateral motor cortices were active during MI of whole-body (vs. upper limbs), while the inferior lateral motor cortices were active during MI of movements with the upper limbs (vs. whole-body).

From an EEG prospective, a few pieces of evidence have shown an inversion of the polarity of the lateralized readiness potential (LRP) during the real and mental execution of hand and foot actions, suggesting similar somatotopic action representation in the motor cortex (Carrillo-de-la-Peña et al., 2006). Furthermore, a classifier technique based on EEG data was used to decode action based on its complexity (Gibson et al., 2014; Yi et al., 2013). For instance, Yi and colleagues (2013) showed that MI of complex action (combination of contralateral upper/lower limbs) resulted in broader ERD in alpha (i.e., 8-11 Hz) and beta (i.e., 18-20 Hz) frequency band over central sites than those (i.e., 8-9 Hz) elicited by simple actions (unilateral limbs). The topographical maps also showed wider distributed ERD on the scalp, reaching the frontal and occipital regions in response to MI of complex movements. Finally, reduced and more focused brain activity was previously found in experts than non-experts during MI of a well-known repertoire of movement (Olsson et al., 2008; Wei and Luo, 2010). It is interesting to note that Di Nota and colleagues (2017) found evidence in opposition to this literature comparing ballet and non-ballet dancers with controls during observation and MI of dance actions. No between-group difference in the alpha peak power or average beta power (13–30 Hz) was found in the MI task, unlike action observation. In our opinion, the lack of modulation during MI might be due to technical issues, including the use of just one sequence of movement repeated several times and the number of MI blocks that varied between participants.

In this study, to clarify the expertise-related different modulation of the AN based on the motor content, a difference wave (DW) was computed for further analysis. ERP evoked by effortful stimuli were subtracted by those evoked by effortless stimuli and plotted on the scalp topographic maps in the two groups. As can be appreciated in Figure 3.24, the differential activity showed a different distribution in the AN time window (400-550 ms) as a function of ballet experience. The DW was more frontally located in controls, while it was more focused over centro-parietal sites in dancers. This result seemed to suggest the occurrence of different imagery processes based on ballet experience. Visuomotor regions might be engaged in dancers, as results of the many hours spent practicing the exact muscular sequence that characterizes each step. In opposition, working memory processes may be required by controls

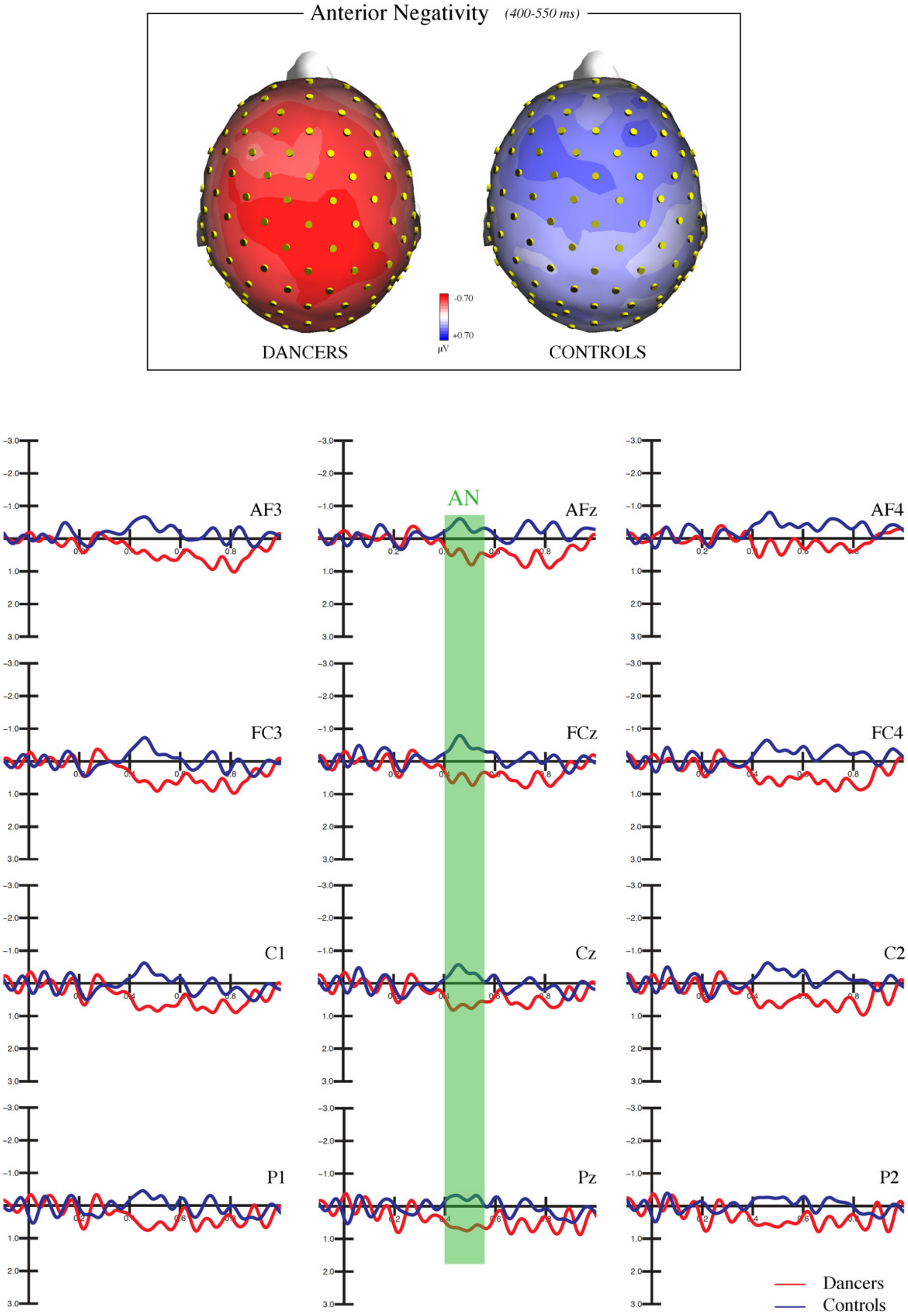


Figure 3.24. Grand average waveforms (*difference wave*) recorded at fronto-centro-parietal sites and topographic map of voltage distribution over the scalp. The topographic map of the scalp voltage distribution computed on the difference wave dancers-*minus*-controls in the AN time window (400-550 ms) is shown in the top of the figure. The positive values of voltage are shown in red, the negative values are displayed in blue. The different colour between group was due to the opposite pattern of results found in dancers and controls. The lower port of the figure illustrates the grand average waveforms (ERPs) of the *difference wave* recorded over fronto-centro-parietal (in red) and controls (in blue).

to perform the MI task, since they have never been exposed to that repertoire of movement before.

Two sources reconstruction swLORETA were performed separately on the two DW, to estimate the neural generators of the AN as a function of the motor content. A list of estimated active dipoles relative to dancers and controls is shown in Table 3.6 and Table 3.7. The main dipoles found in the experts were localized in the fusiform and inferior/middle temporal gyri (BA 20, 21, 37), while the non-experts showed greater activity in the prefrontal (BA 10, 11, 47) regions (see Figure 3.25). These results were consistent with greater activity in the right fusiform gyrus (BA 20) and left hippocampus found in the brain of expert divers during repertoire specific MI task (Wei and Lou, 2010). In this regard, the OTC includes regions selectively activated by the observation of body, face, and motion that are also sensitive to action content (Ma et al., 2018; Tucciarelli et al., 2015). The enhanced engagement of this regions was previously linked to the refined ability to used body information to predict the outcome of an action in experts (Abreu et al., 2012; Aglioti et al., 2008). Abreu and colleagues (2012) also found the engagement of the anterior insular cortex when the experts were correctly predicting the outcome of game action, likely indexing increased bodily awareness.

At the same time, the orbitofrontal cortex (OFC) was here recruited by non-experts, suggesting high-order processes to predict the outcome. Activity in this region (in addition to the cerebellum and PPC) was previously found in individuals with poor (than good) imagery ability (Guillot et al., 2008) and linked to memory formation due to its connections with the parahippocampal regions (Frey and Petrides, 2002). For instance, Frey and Petides (2002) showed increased activity in the right OFC and parahippocampal areas while the participants were watching abstract images with increasing encoding demands (i.e., from passive observation to active encoding). In this regard, both our groups of participants showed activity in the left uncus/STG (BA 28/38), part of the parahippocampal gyrus. Activity in this region was shown during MI of fingers movements (Burianová et al., 2013), repertoire specific actions (Wei and Luo, 2010), but also for recalling of consolidated autobiographical memories (Zeidman and Maguire, 2016) and natural scene (Zeidman et al., 2015). Specifically, experts showed bilateral recruitment of the uncus/STG along with right posterior cingulate cortex (PCC, BA 23), regions that are part of the limbic system and have been linked to emotional response to the human body (Proverbio et al., 2014; Vocks et al., 2010c). For instance, Proverbio and colleagues (2014) found increased uncus response during the observation of affective body postures that were incongruent (than congruent) with short verbal descriptions of the relative emotion. Activity in the PPC was also found during locomotor MI (Malouin et al., 2003) and linked to spatial attention (Mesulam et al., 2001). In the present study, different recruitment of sensorimotor regions (BA 6, 40) was also found according to ballet experience, with controls showing right lateralization and professionals showing activity in both left (precentral gyrus, BA 6) and right (IPL, BA 40) hemisphere. A large amount of evidence showed the role of the premotor and parietal cortex during mental imagery of actions (Hétu et al., 2013; Pilgramm et al., 2016; Ptak et al., 2017). Pilgramm and colleagues (2016) used 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. This result suggested that these brain areas played a key role in the cognitive representation of the motor content during MI. Engagement of PPC, SMA, and PM has also been linked to motor awareness and conscious intention (Desmurget and Sirigu, 2009; Desmurget et al., 2009). For instance, intracranial electric stimulation of the right IPL led to desire and intention to move the contralateral limb (Desmurget et al., 2009). Increased stimulation intensity also resulted in the belief that an actual movement was executed. Finally, the modulation of the activity of the left PPC (BA 40) shown by a few authors after motor imagery training suggested the importance of this cortical region in action representation (Lebon et al., 2018; Olsson et al., 2008).

Overall, the evidence found in our study seemed to confirm that different processes might occur in the two groups during MI. Increased cognitive load in controls was likely the results of the greater amount of kinematic information conveyed by effortful (than effortless steps) that the participants had to codify, remember, and recall. Contrarily, enhanced OTC, PM, and IPL activity in dancers while watching effortless movements might suggest retrieval of body-related and sensorimotor information. It is possible to hypothesize that the motor program underling effortful jumps, turns, and steps were more automatized in ballet experts, as suggested by the decreased AN amplitude. Further studies will be required to investigate the MI processes as a function of expertise and motor content, including for instance the ability to explicitly encode and recall action details.

In conclusion, in the present study, we showed that ERPs are a good technique for investigating kinaesthetic motor imagery processes. Previous studies have compared EEG modulation (ERD and LRP) evoked by MI with the real execution of movement. Here, we found an anterior negativity (AN) response (400-550 ms) during the MI of whole-body complex action, following a motor imagery training. This component was specifically modulated by the expertise level of the participants with the dance steps they had to imagine. Increased frontal activity was found in dancers but not non-dancers, likely due to motor knowledge of the dance steps. Moreover, the AN was modulated by the motor content in an expertise-related manner. Larger negativity and recruitment of prefrontal areas was found in response to effortful movements in the brains of non-experts. This result likely suggested greater cognitive load/effort in the brains of individuals without motor representation of the imagined action. At the same time, enhanced AN and engagement of body-related and sensorimotor regions was shown during MI of effortless movement in the experts. Thus, professional dance practice might have led to enriched and refined action representation processes involved in mental action execution.

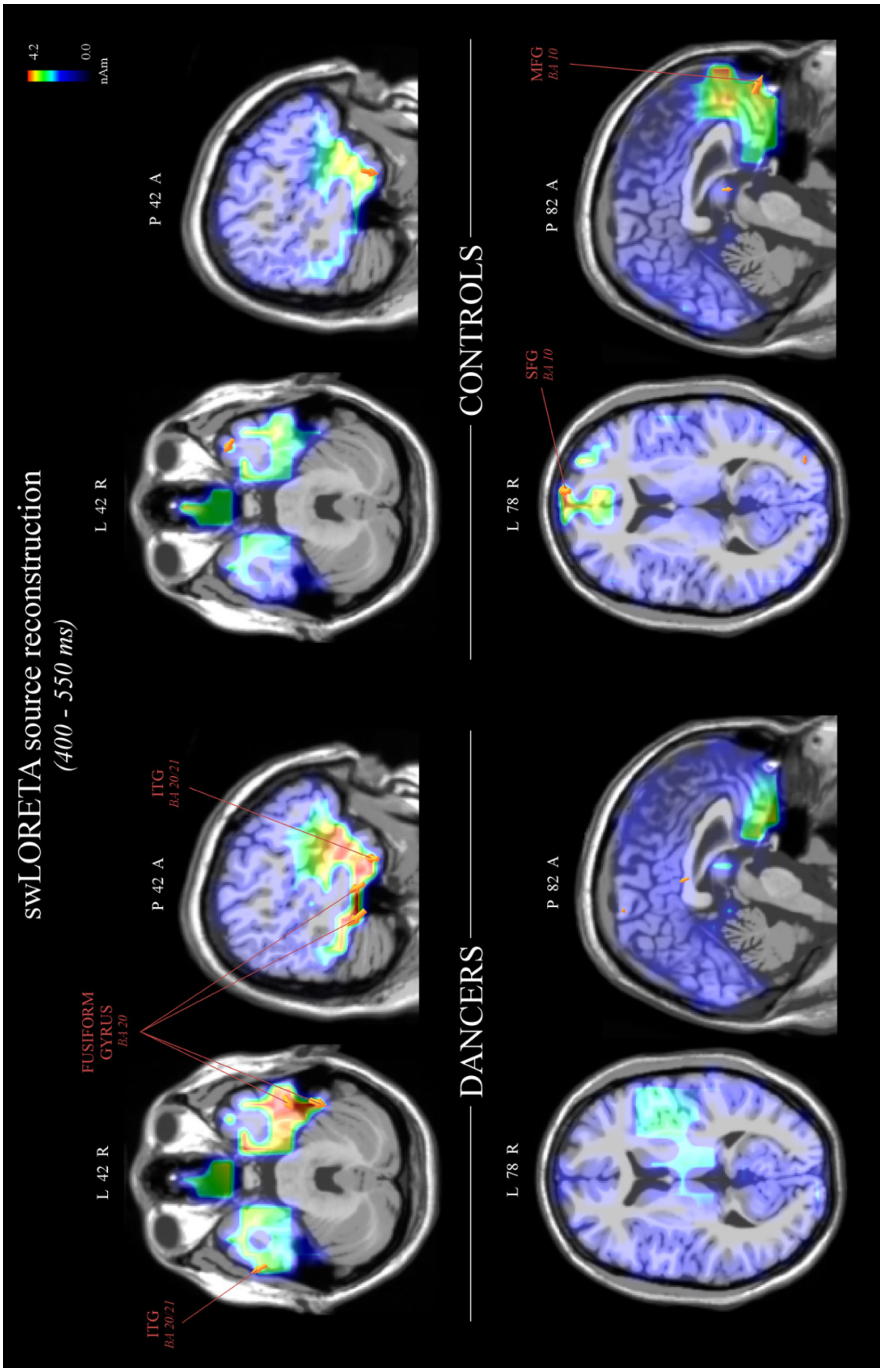


Figure 3.25. SwLORETA source reconstruction of surface potentials in the AN time window (400-550 ms). SwLORETA performed on the *difference wave* obtained by subtracting the ERPs elicited by effortless stimuli from those elicited by effortful stimuli (in the LP time window 1400-1600 ms) in dancers (left part of the image) and controls (right part of the image). The axial and sagittal anatomical planes of the brain are shown. The activation of the right fusiform gyrus (BA 20) and bilateral inferior tempora gyrus (ITG, BA 21)he left inferior temporal gyrus (ITG, BA 20/21) is visible in the brain of dancers. The activation of the right superior frontal gyrus (SFG, BA 10) in the brain of the controls can also be appreciated. The strongest magnitude values of the signal (nAm) are shown in red.

Chapter 4

Neural representation of time dynamics in dance action: an fMRI study

«Time is an illusion»

Albert Einstein

4.1. Introduction

The aim of this last experimental chapter was to investigate the encoding of the acceleration in action representation. The brain activity of non-dancers participants was compared during the observation of contemporary dance movements that varied along the time dimension. Two categories of video stimuli were created by instructing one professional dancer to reproduce the same sequences of steps with different acceleration profiles. Firstly, he performed the sequences in a fluid, Tai Chi-like manner, trying to keep unchanged the acceleration and speed of the movements (uniform acceleration). Secondarily, he reproduced the same sequences by varying as much as possible the acceleration of the steps (varied acceleration), thus, introducing pauses, accelerations, and decelerations. As a result, it was manipulated "how" the action was performed, but not its semantic content ("what"). Moreover, long sequences of dance movements were used instead of short video clips representing single steps to guarantee a more ecological and naturalistic observation. The study has been conducted at the SoBA (Social Brain in Action) of the University of Glasgow run by Prof. Emily Cross, in collaboration with Dr. Guido Orgs (Goldsmiths, University of London) and Prof. Alice Mado Proverbio.

A growing number of authors have been investigating the neural correlates of action observation in naïve viewers using complex dance movements as an object of study (Pollick et al., 2018; Vaessen et al., *in press*). Recently, specific focus has been given to the impact that dance kinematics have on the emotional communication (Christensen et al., 2016) and modulation of the AON (Noble et al., 2014). A case in point was the fMRI study by Noble and colleagues (2014), in which non-dancer participants were presented with a long video depicting a female dancer performing Classical Indian Dance. The overall body motion of the dancer was quantified with an algorithm and used as a parametrical regressor. The activity of the right ITG (possibly the EBA) showed a modulation based on the variation of the motion index. Moreover, in a previous behavioral study of the same research team, a different group of volunteers was instructed to segment the long dance video in single events perceived to have a beginning and an end. When these results were introduced in the fMRI model, activity in the right inferior occipital gyrus, left middle occipital gyrus and right IFG was associated with event segmentation. This evidence showed a role of right fronto-temporal regions in the analysis of dynamic changes in body motion and a hierarchical action representation in the prefrontal areas. More recently, Vaessen and colleagues (in press) studied the neural substrates of action perception using a computational model that hierarchically distinguished between low, midlevel and high-order features. They presented the non-dancer volunteers with two categories of dance videos depicting "lightness" and "fragility" during fMRI scanning. A multi-voxel decoder based on a Gaussian Naïve-Bayes classifier showed a discrimination ability between conditions in the lingual gyrus/calcarine sulcus (i.e., left occipital pole, MOG, and calcarine sulcus bilaterally) and SPL/IPS. Moreover, an RSA (*representational similarity analysis*) analysis was used to investigate the impact of specific features of the stimuli on the brain activity. Low-level features (i.e., acceleration, magnetic moment, and symmetry) modulated the activity of the early visual regions (MOG and superior medial parietal cortex) while the midlevel features (i.e., lightness) affected the response of the OTC (EBA and hMT+), IPL and pSTS. Thus, the authors suggested a perception of body movement based on organized feature statistics rather than semantic categories.

From an electrophysiological perspective, Poikonen and colleagues (2018) showed a modulation of the synchrony in the alpha frequency band as a function of the variation of the acceleration of dance steps. The participants were presented with videos of a dancer or stick figure performing a contemporary dance piece with or without music. A motion capture technology was used to quantify the acceleration of the dancer and create the two categories of movements (high vs. low acceleration). The segments of the dance characterized by high acceleration included large fast movements (i.e., jumps, turnings, vast arm, and leg movements). The pieces of the dance characterized by low acceleration included slow steps and standing with minor movements. In all the volunteers' EEG (regardless of their expertise with dance or music), high acceleration (than low acceleration) movements resulted in decreased synchrony in the alpha range (8-13 Hz). The distribution of this effect was broader during the observation of the dancer accompanied by the music, rather than the dancer alone or the sticky figure. The anterior desynchronization (mu rhythm) was attributed to the increased amount of motion (visuomotor resonance), while the posterior desynchronization was interpreted as an index of enhanced attention towards the movements.

In the studies on acceleration encoding presented so far (Noble et a., 2014; Poikonen et al., 2018; Vaessen et al., *in press*), the stimuli characterized by high vs. low acceleration were not balanced for a number of factors. This included the use of the space by the dancer, movements reproduced, body parts used, emotional content, and low-level kinematics. In the present investigation, the two categories of movements showed to the participants represented the same dance sequences, merely varied for the changes in the acceleration (varied acceleration vs. uniform acceleration). This allowed a more refined control of possible confound variables.

At this point, it is interesting to consider the fMRI study by Casile and colleagues (2009) on the encoding of action invariants during movement observation. Human movements are characterized by several kinematics laws. One of these is referred to as "two-thirds power law" (Lacquaniti et al., 1983) and expresses the exponential relationship between the tangential velocity and the curvature, during a curvilinear path. Casile and colleagues (2009) presented the participants with videos depicting a human avatar reproducing curvilinear letters written in the air (i.e., “lle”, “leo”) using both hands. In one condition, the movements complied with the kinematic law, showing reduced speed in the curvilinear than rectilinear tracts. In another condition, the stimuli were altered to violate the two-thirds power law, being uniform in the speed. The observation of the natural action selectively engaged the left dorsal PM, middle and superior frontal gyri and medial frontal cortex. No specific activity was found in response to the perturbated movements. These results showed a fine-tuning of the premotor and frontal areas toward familiar human action that followed the kinematic law of motion.

The visuomotor system would also be capable of discriminating between the natural and reversed playback direction of action, likely due to acquired familiarity with the forward movements. For example, Maffei and colleagues (2015) presented the participants with short videos of an actor walking from side to side in a forward and backward direction, in both normal (original) and reversed (time inversion) versions. A higher discrimination ability was found for the forward walking (greater for the natural than reversed condition) than backward walking. Specifically, the discrimination of the latter condition was at a chance level. The observation of backward video also elicited stronger activity in the temporo-occipital junction (TOJ) than the forward version of the same stimuli, likely indexing a discrepancy between expected and real input (familiarity). Activity was also found in the intraparietal sulci and right STS only when a discrimination judgment was required, but not during passive observation. The left FG, right precuneus and ACC were instead active while watching normal compared with reversed videos.

A final point to consider concerns the brain areas that showed sensitivity to action timing. A review of the literature on time perception by Grondin (2010) showed converging evidence from behavioral, EEG, and imaging studies for several cortical and subcortical regions engagement in time processing. This included the cerebellum, frontal areas (i.e., dorsolateral prefrontal cortex - DLPFC and SMA), right PPC, and basal ganglia. In this regard, Hasson and colleagues (2008) showed evidence for a hierarchy of cortical regions sensitive to different temporal receptive windows. The authors presented twice the participants with videos depicting classical silent films in a forward, backward, or scrambled playback direction. The clips could also have a short (3-5 seconds), intermediate (9-15 seconds) or long (32-40 seconds) timescale. The reliability of brain responses within each condition was interpreted as an index of preferential activity. The early visual cortices (i.e., V1, LO, and hMT+) showed a similar response regardless of the playback direction and length of the movies. Higher reproducible responses were obtained in high order cortical areas as a function of the direction playback and timescale. Selectivity of the posterior lateral sulcus, TPJ, and frontal eye field was found in response to long duration clips while the STS and precuneus were active for intermediate durations. In these regions, greater activity was also found for forward than backward and scrambled stimuli.

In the present study, non-dancer volunteers were shown videos of a professional male dancer performing 12 sequences of whole-body complex contemporary movements varying along the time dimension. The neural activity in response to dance sequences characterized by uniform/constant acceleration was compared with that elicited by the same sequences defined by changes/variations in the acceleration. The reversed playback version of the same videos was also used as a control condition to keep unvaried the low-level features of the stimuli, such as the length and kinematics (Casile et al., 2009; Viviani et al., 2011), resulting in a 2 x 2 design. The videos were repeated four times while the participants were instructed to report their ratings for enjoyability or feasibility for each clip. At the end of the fMRI scanning, all stimuli were presented once again to the volunteers that were engaged in a discrimination task. They were asked to detect and indicated the playback direction of each dance sequence (forward vs. backward) to assess their ability to perceive the difference between the two conditions. The study aimed to investigate the encoding of the acceleration in action representation during the aesthetic perception of dance sequences as a function of timing variation and familiarity (playback).

On the basis of the actual literature, we hypothesized to find greater engagement of the occipito-temporal cortices, including the EBA and hMT+ (Noble et al., 2014), and of the visuomotor regions, such as the PM, DLPFC, and PPC (Casile et al., 2009; Poikonen et al., 2018) in response to dynamic/varied rather than fluent/uniform moves, characterized by a higher ME score. Moreover, we assumed to find a modulation of the activity of those brain regions that showed to be sensitive to action timing (Grondin et al., 2010), including the cerebellum, SMA, and basal ganglia. No main difference between forward and backward videos would be expected at an early stage of processing (i.e., V1, hMT+), since forward and backward moves share same low-level visual features (Hasson et al., 2008). Finally, a modulation of the response of biological motion selective regions would be expected as a function of video playback, including the STS, precuneus (Hasson et al., 2008), TOJ (Maffei et al., 2015), EBA and PPC (Costantini et al., 2005).

4.2. Methods

4.2.1. Participants

Twenty-nine right-handed volunteers participated in the present study. They were between 19 and 36 years of age (mean age: 23.61 years, SD = 4.02) and had normal or corrected-to-normal vision. Specifically, 11 of them were males (mean age: 26.36 years; SD = 4.3) while the other 19 were females (mean age: 23.61, SD = 4.02). The volunteers reported no history neuropsychology disorder or drug abuse. Their right-handedness was assessed using the Edinburgh Handedness Inventory (mean index score: 0.77, SD = 0.22). Each volunteer received 12£ for his/her participation (that took no more than 2 hours). The study was approved by the ethical committee of the University of Glasgow, and all participants signed the informed consent before initiating the experiment.

4.2.2. Stimuli

Twenty-four different grayscale videos were used as stimulus material in the present fMRI study. Each clip depicted a professional male dancer performing a sequence of complex whole-body movements. Specifically, 12 fragments from work ‘Duo' by William Forsythe were recorded in a double version. First, the dancer was instructed to execute them in fluid, smooth way, keeping the acceleration and speed as uniform as possible (*uniform*). Subsequently, he was asked to execute the same sequences by repeatedly changing the acceleration of the movements (*varied*), introducing pauses, accelerations, and decelerations. Thus, 12 video pairs were obtained, each depicting the same actions' sequence, varying as a function of the acceleration. The dancer performed at the center of the scene in all the stimuli, starting and ending each sequence in a relaxed standing position (with his arms along the body). The rehearsal room was empty, and the luminance condition was constant during the recordings. The stimuli were recorded in Full HD (1080i: 1920x1080 pixels) with a frame rate of 25 fps. In a post-production phase, all the clips were silenced, and 12 frames of fade-in and fade-out from and to black were added at the beginning and end of the videos respectively. The final version of the stimuli had a duration between 8.64 and 15.68 seconds (mean duration: 11.78 seconds, SD = 2.00). Particularly, t-test for independent samples showed a significant difference in stimuli duration as a function of dynamics factor [t(22) = 5.998, $p < 0.0001$]. Uniform videos (13.32 minutes, SD = 1.15) were significantly longer than varied videos (10.24 minutes, SD = 1.38). Furthermore, a variated version of the 12 pairs clips was created by reversing their playback direction (backward movements), using Adobe Premiere Pro CC 2015 (v. 9.0) software. These backward stimuli were used as a control condition for the forward natural videos since the low-level visual features (i.e., action kinematics) and duration of this videos were identical between each pair. Thus, a total of 48 videos was used in the present investigation (see Figure 4.1).

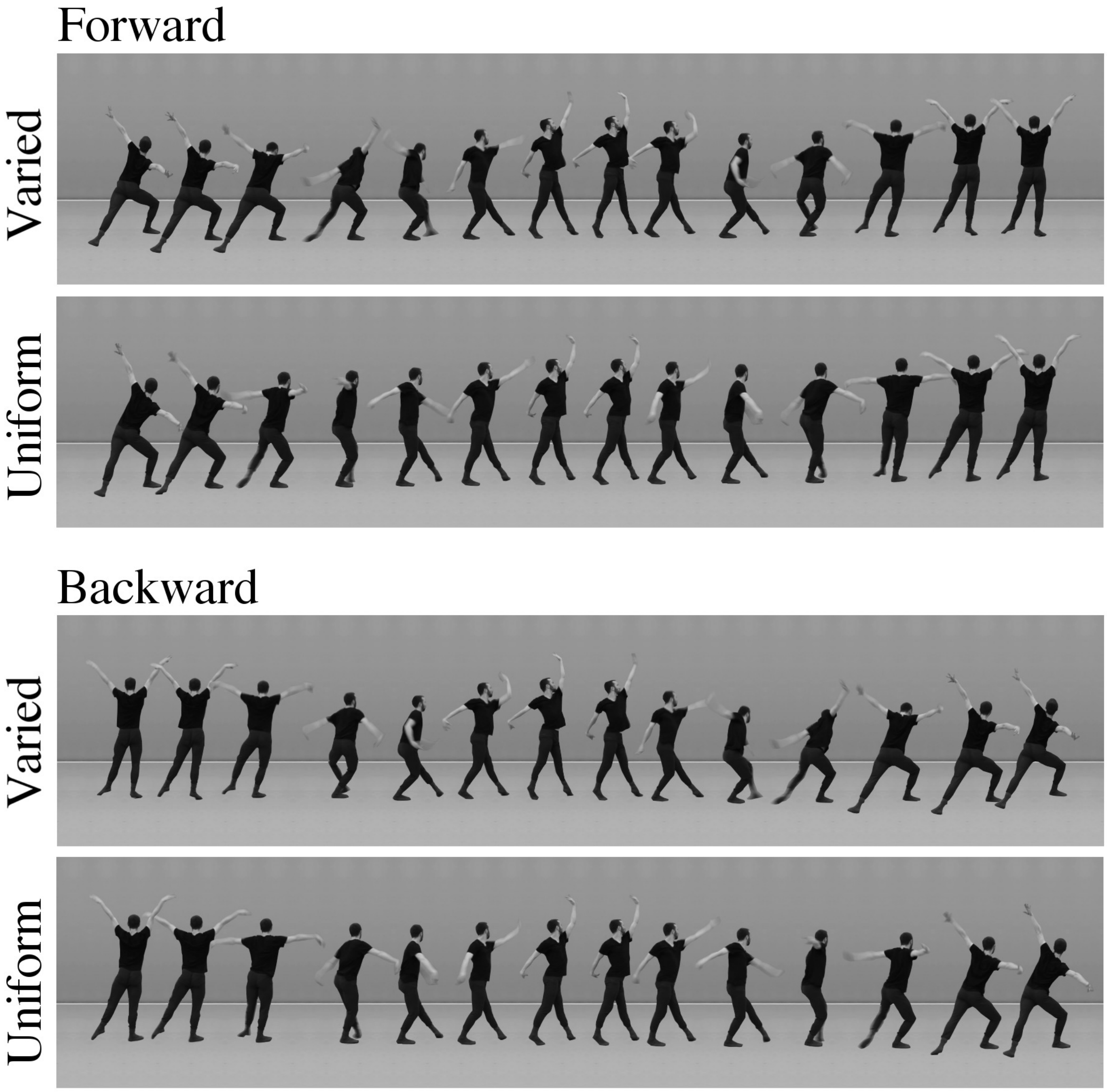


Figure 4.1. Example of stimuli. Fourteen static frames were taken from a video at different temporal stages and placed side by side to illustrate the difference between the four categories of movement. The upper part of the image shows a fragment of a forward sequence. The lower part of the image shows the backward version of the same fragment.

4.2.3. Kinematics computation

Motion Energy Quantification

To quantify the actual difference in the kinematics of the varied and uniform movements motion energy (ME) quantification was performed. A MATLAB (2017b version) algorithm based on motion recognition work in computer science (Bobick et al., 1997) was used. A difference image for pairs of consecutive frames was computed on each video so that any pixel with more than 10 units luminance change was classified as "moving." The average numbers of moving pixels per frame and movie were summed to give a motion energy score for that clip (Cross et al., 2012). Given that the camera was fixed, the body was the only moving element of the screen. The floor and background were stationary. Thus, the motion energy quantification was relative to the moving body of the dancer only. Subsequently, a 2x2 repeated measure ANOVA was performed on the ME values for each stimulus, with dynamics (uniform, varied) and playback direction (forward, backward) as within-subjects factors. A main effect of dynamics factor [F(1,11) = 200.562, $p < 0.0001$] was shown. Contrarily, neither the playback direction factor ($p = 0.41$) or interaction between the two factors were significant ($p = 0.24$). This result confirmed that the varied videos were characterized by a greater amount of kinematic information compared with the uniform videos. At the same time, the lack of any further significance indicated that the backward stimuli represented a good control condition for the forward stimuli (same length and kinematics) since no difference between forward and backward movements was found (see Figure 4.2).

Offline Motion Tracking

A more refined and precise measure of the action timing conveyed by the forward and backward videos was obtained by mean of an offline motion tracking technique. Tracker 5.0.2 software was used for this purpose. Each original forward video was manually processed by placing four markers on the wrists and ankles of the dance, in a frame-by-frame approach. The height of the dancer (1.75 meters) was used as the reference to calibrate the measurement system. Thus, speed and acceleration profiles of the four limbs were computed for all the forward videos as a function of the time, along with the trajectory of the body in 2D space. Then, all measurements for speed and acceleration were collapsed into two distinct mean values for each limb and used for statistical analysis. They were subjected to multifactorial repeated measures ANOVA (performed using Statistica version 10 software by Statsoft) with three within-groups factors, including movement dynamics (uniform, varied), body side (left, right) and limbs (upper, lower) factors.

Speed profile

ANOVA performed on the speed values showed a main effect of dynamics factor [F(1, 11) = 119.581, $p < 0.0001$], suggesting that varied movements (1.02 m/s, SD = 0.07) were faster than uniform movements (0.66 m/s, SD = 0.06).

Movements performed with the upper limbs (1.15 m/s, SD = 0.10) were more faster than those performed with the lower limbs (0.53 m/s, SD = 0.05), as shown by the significance of limbs factor [F(1, 11) = 33.631, $p < 0.0002$].

The further dynamics X limbs interaction [F(1, 11) = 21.360, $p < 0.001$] and relative Tukey post-doc test confirmed that varied movements were faster than uniform movements using both upper (varied: 1.40 m/s, SD = 0.11; uniform: 0.90 m/s, SD = 0.10; $p < 0.0002$) and lower limbs (varied: 0.64 m/s, SD = 0.06; uniform: 0.43 m/s, SD = 0.04; $p < 0.003$).

Lastly, the difference between upper and lower limbs was visible for both left (upper: 1.03 m/s, SD = 0.12; lower: 0.56 m/s, SD = 0.07; $p < 0.0003$) and right (upper: 1.26 m/s, SD = 0.10; lower: 0.51 m/s, SD = 0.08; $p < 0.0002$) body side, as suggested by the significant limbs X body side interaction [F(1, 11) = 8.230, $p = 0.016$].

Overall, the reproduction of the original (varied) dance sequences in the fluent and smooth (uniform) version resulted in slower movements using both the arms and legs.

Acceleration profile

ANOVA performed on the acceleration values showed a main effect of dynamics factor [F(1, 11) = 89.317, $p < 0.0001$], suggesting greater accelletation in varied (7.81 m/s^2, SD = 0.61) than uniform (3.82 m/s^2, SD = 0.26) movements.

Movements performed with the upper limbs (7.47 m/s^2, SD = 0.60) were characterized by greater accelleration than those performed with the lower limbs (4.16 m/s^2, SD = 0.42), as shown by the significance of limbs factor [F(1, 11) = 28.776, $p < 0.0003$].

The further dynamics X limbs interaction [F(1, 11) = 16.508, $p < 0.002$] and relative Tukey post-hoc test confirmed that varied movements were more accelerated than uniform movements using both upper (varied: 1.40 m/s^2, SD = 0.11; uniform: 0.90 m/s^2, SD = 0.10; $p < 0.0002$) and lower limbs (varied: 0.64 m/s^2, SD = 0.06; uniform: 0.43 m/s^2, SD = 0.04; $p < 0.003$).

Lastly, the difference between upper and lower limbs was visible for both left (upper: 6.63 m/s^2, SD = 0.54; lower: 4.23 m/s^2, SD = 0.0.54; $p < 0.009$) and right (upper: 8.32 m/s^2, SD = 0.71; lower: 4.09 m/s^2, SD = 0.59; $p < 0.0003$) body side, as suggested by the significant limbs X body side interaction [F(1, 11) = 4.855, $p < 0.05$].

Overall, the reproduction of the original (varied) dance sequences in the fluent and smooth (uniform) version resulted in movements characterized by reduced acceleration using both the arms and legs (see Figure 4.3).

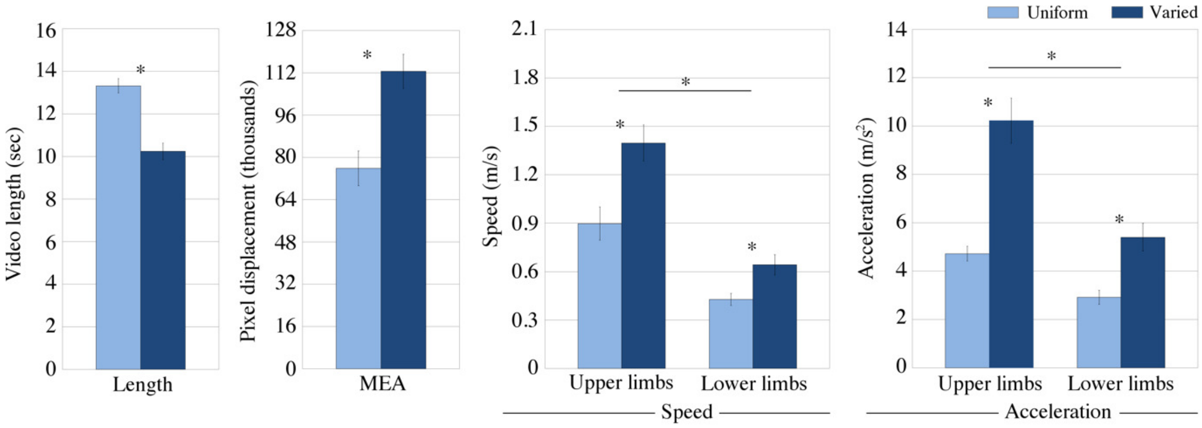


Figure 4.2. Kinematics computation. The histograms (from left to right) respectively display the length (in seconds), the Motion Energy quantification (MEA), the speed and acceleration prifile (by mean of the offline motion tracking technique) of the uniform and varied video categories. The varied version of the dance sequences (dark blue) were caracthterized by an overall higher motion energy than the unifrom version of the same movements (light blue). More specifically, the movements of the dancer were faster and higher in acceleration in the dynamic/varied stimuli version. This difference was visible with both upper and lower limbs.

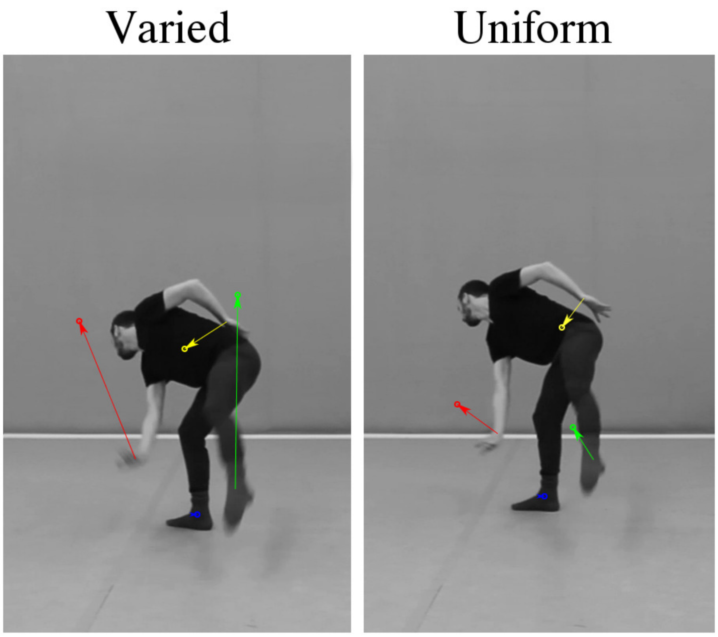


Figure 4.3. Example of acceleration. The figure shows two frames of the same movement belonging to a varied (left) and uniform (right) sequence. The colours arrows represent the acceleration vectors computed by the offline motion tracking software for the four limbs. The length of the arrows indicated the scalar value of the acceleration (x5 magnified for representational purposes), being larger in the varied than uniform condition.

4.2.3. Stimuli validation

To assess whether non-dancer participants would be able to perceive the difference in speed, acceleration, and muscular effort required by the uniform and varied movements, a validation study was carried out. Forty-one volunteers took part in this behavioral study (10 males and 31 females). They were aged between 18 and 23 years (mean age: 20.20, SD = 1.36) and reported no formal training with dance. Only a few volunteers indicated previous amatorial dance practice (mean experience: 1.41 years, SD = 2.74). The participants were invited twice in the lab once week apart and presented with a behavioral rating task. Two sessions were created to avoid habituation effects due to stimuli repetition and attention drops. In both of them, all 48 different videos (12 uniform forward, 12 uniform backward, 12 varied forward, 12 varied backward) were presented twice at the centre of the screen (with a resolution of 1029 x 1080 pixels) and followed by one out of two questions (using OpenSesame software version 3.1.9). Specifically, in the first session, they were instructed to observe each video and rate the amount of speed (*Please rate the SPEED of the movements in this video*) or effort (*Please rate how much EFFORT is required to perform the movements in this video)* that characterized the dance sequence (see Figure 4.4). In the second session, they were asked to rate the feasibility (*Please rate how well you could REPRODUCE the movements in this video*) and enjoyability (*Please rate how much you ENJOYED watching the movements in this video*) of each move. Four different runs of 24 stimuli each were created (96 stimuli per session), the stimuli were presented in a pseudorandomized order. The same video was never presented more than once in each run, and different questions were asked when a different version (forward vs. backward; uniform vs. varied) of the same sequence was proposed (i.e., video 1: uniform forward – Effort; varied backward - Speed). The prompt with the question remained on the screen until keypress. The volunteers could express their rating for each factor using a 5-point Likert scale (1 = very little; 5 = very much) by pressing the correspondent key on a computer keyboard. The participants that showed mean ratings and years of expertise that exceeded ± 2SD (standard deviation) were considered outliers are removed from the analysis. Base on this criterion, data from thirty-two volunteers were used for the analysis. Furthermore, due to a technical error, only the ratings for 11 out of 12 dance sequences were recorded and subsequently analyzed. Distinct repeated measure ANOVA with two within-subjects factors (dynamics: uniform, varied; playback direction: forward, backward) was performed on the mean rating values for effort, speed, feasibility, and enjoyability. Correlations between the values of the four scales of interest factors were also performed. The discussion of the results relate to the aesthetic perception (likability) of dance actions is beyond the scope of the present thesis. In this regard, neuroaesthetics implication of this evidence won't be taken into consideration here.

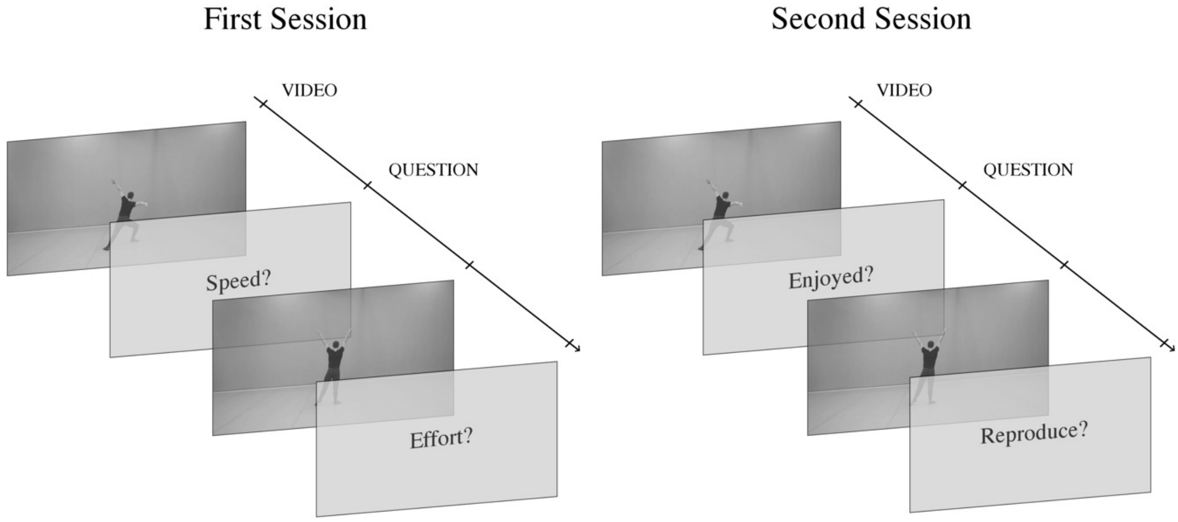


Figure 4.4. Timescale of the validation experimental design. Each trial consisted in a counterbalanced presentation of videos depicting the uniform or varied version of dance sequences in both forward and backward playback direction. After the video offset, a keyword (question) remained on the screen until button press. The volunteers were invited in the lab two times for two different session (one week apart). They were instructed to rate each video for the perceived speed and effort during the first session. They were asked to rate the same videos for the perceived feasibility and enjoyability during the second session.

Validation results

ANOVA performed on the speed rating values showed that varied movements (3.55, SD = 0.05) were perceived as faster than uniform movements (2.53, SD = 0.07), as indicated by the significant dynamics factor [F(1, 31) = 259.318, $p < 0.0001$]. See Figure 4.5.

ANOVA performed on the effort rating values showed that varied movements (3.46, SD = 0.06) were perceived as more effortful than uniform movements (2.80, SD = 0.07), as indicated by the significant dynamics factor [F(1, 31) = 162.528, $p < 0.0001$]. The further dynamics X playback interaction [F(1, 31) = 7.405, $p < 0.02$] and relative Tukey post-hoc test showed that forward uniform movements (2.87, SD = 0.08) were perceived as more effortful ($p < 0.024$) than backward uniform movements (2.72, SD = 0.07). No difference was found for varied moves ($p = 0.85$).

ANOVA performed on the feasibility rating values showed that varied movements (2.48, SD = 0.10) were perceived as more difficult to reproduce than uniform movements (2.98, SD = 0.11), as indicated by the significant dynamics factor [F(1, 31) = 61.691, $p < 0.0001$].

ANOVA performed on the enjoyability rating values showed that varied movements (3.43, SD = 0.08) were perceived as more enjoyable to observe than uniform movements (2.95, SD = 0.09), as indicated by the significant dynamics factor [F(1, 31) = 51.897, $p < 0.0001$].

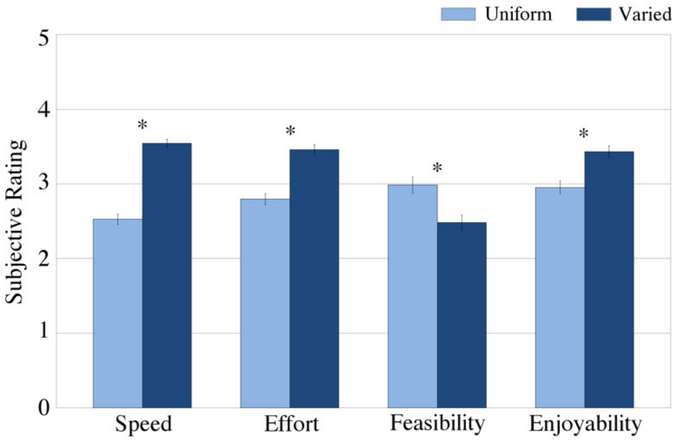


Figure 4.5. Subjective ratings. The histogram shows the results of the validation procedure. The varied dance sequences (dark blue) were perceived as faster, effortful, difficult to reproduce, and more enjoyable to watch than the uniform version (light blue) of the stimuli.

Finally, the positive correlation between speed and effort [r = 0.80, $p < 0.0001$] showed that faster (than slower) movements were judged as more effortful. At the same time, the negative correlations between feasibility and either speed [r = -0.33, $p < 0.0002$] and effort [r = -0.38, $p < 0.0001$] showed decreasing ratings in reproducibility with increasing action speed and muscular effort. Finally, a positive correlation was shown between enjoyability and both effort [r = 0.410, $p < 0.0001$] and speed [r = 0.45, $p < 0.0001$], while it was negatively correlated with the feasibility ratings [r = -0.25, $p < 0.005$]. Namely, the participants enjoyed more watching the dance videos perceived as faster, effortful and difficult to preproduce (see Figure 4.6).

Overall, the dance sequences characterized by greater variation in acceleration and speed (compare with uniform/fluent sequences) were perceived as more fast, effortful, enjoyable to observe, but difficult to reproduce. No effect of video playback was expected on speed ratings because backward and forward videos were characterized by the same speed (the reason why backward stimuli were chosen as a control condition). The evidence suggested that the playback direction also had no impact on the feasibility and enjoyability ratings. However, the complexity of the stimuli could have made it difficult to discriminate between the forward and backward directions. To test this idea, a discrimination task was introduced at the end of the main fMRI experiment, as described in the next paragraph.

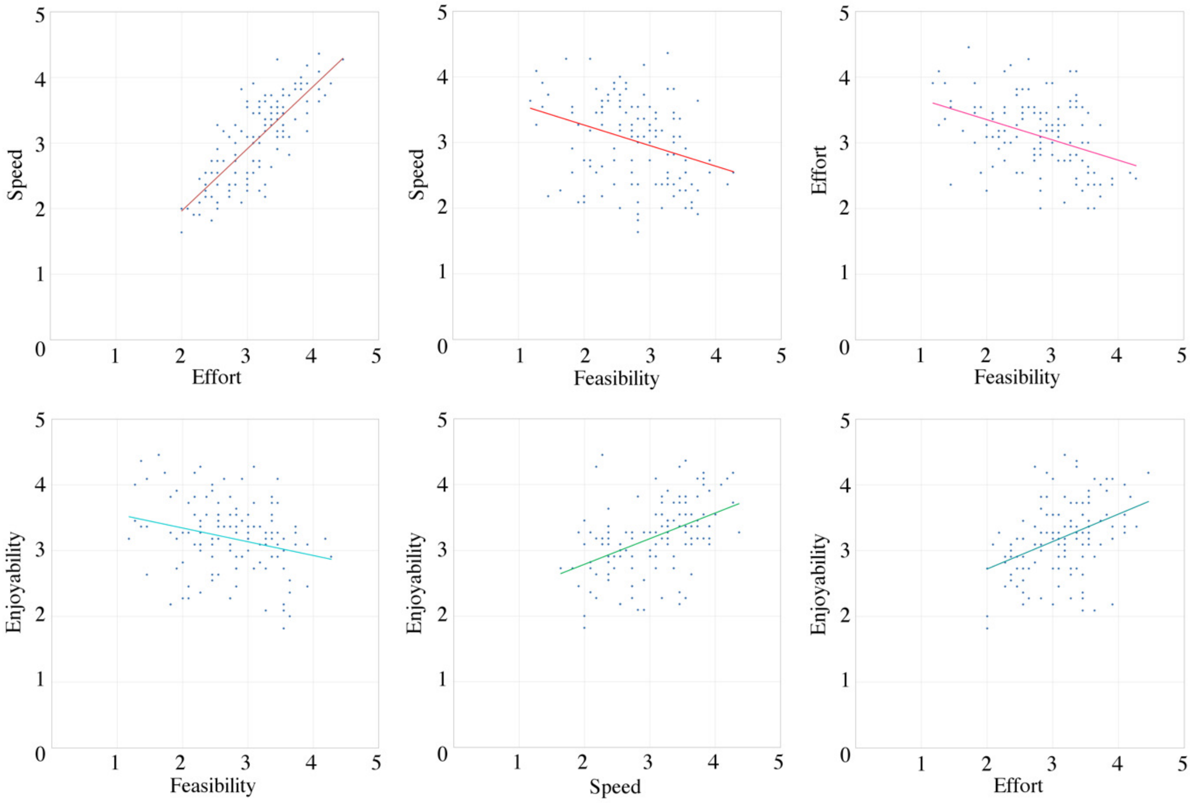


Figure 4.6. Correlations between the subjective ratings. The figure shows the significant Pearson's r correlations between pairs of factors. A positive correlation was found for speed vs. effort (1st plot), speed vs. enjoyability (5th plot), and effort vs. enjoyability (6th plot). A negative correlation was shown for speed vs. feasibility (2nd plot), effort vs. feasibility (3rd plot), and enjoyability vs. feasibility (4th plot).

4.2.4. Task and Procedure

The participants completed the fMRI security check before entering the scanner to prevent the presence of metal objects over (and on) their bodies or the compliance with any of the exclusion criteria. Then, the experimenter made them lie down on the scanner's patient table. They were provided with earplugs and instructed how to use the 4-buttons response box. 6 functional runs were created, each composed by 33 trials (and lasting 10 minutes). Figure 4.7 shows the timescale of the experimental design. One functional trial was composed by the presentation of a black fixation cross (on a light grey background) for an interval (ISI) between 2 and 4 seconds (logarithmical distributed); a video (between 8.64 and 15.68 seconds in duration); a question lasting 4 seconds ("*Enjoyed?*", "*Reproduce?*"). The participants were instructed to observe carefully each video and to rate the feasibility (*"How well do you think you can reproduce this movement"*) or enjoyability (*"How much did you enjoy watching this video?"*) of it. They could express their ratings using a 4-point Likert scale (1 = very little; 4 = very much) by pressing the corresponding button on a 4-buttons response box. The question disappeared as soon as one button was pressed, and it was replaced by an empty light grey screen (until reaching the 4 seconds). Furthermore, the 6 runs were divided into two different sessions lasting approximately 35 minutes each. The order of presentation of the 6 sequences was counterbalanced between participants. The video stimuli were presented with a resolution of 1024 × 576 pixels (37 x 21 cm) using a back-projection system, which incorporated an LCD projector that projected onto a screen placed behind the magnet. The screen was reflected on a mirror installed above participants' head birdcage, corresponding to a distance of 110 cm between the screen and the participants' eyes. Overall, the videos subtended a visual angle of 19° 5' x 10° 54'.

At the end of the scanning session, the participants were invited to fulfill a few questionnaires to assess their right-handedness (Edinburgh Handedness Inventory) and previous expertise with dance (an Index developed at the Goldsmiths University of London). They were also engaged in a short behavioral task (lasting approximately 12 minutes). All the 48 different videos were presented at the center of the screen in a pseudorandomized order, using the OpenSesame software. Each video was followed by the word "*Direction?*". The volunteers were instructed to indicate (discrimination task) whether the sequence of movements was reproduced in an original/natural/forward direction or a modified/reversed/backward direction. They could express their preference by pressing the relative *F* (forward) or *B* (backward) key on the computer keyboard.

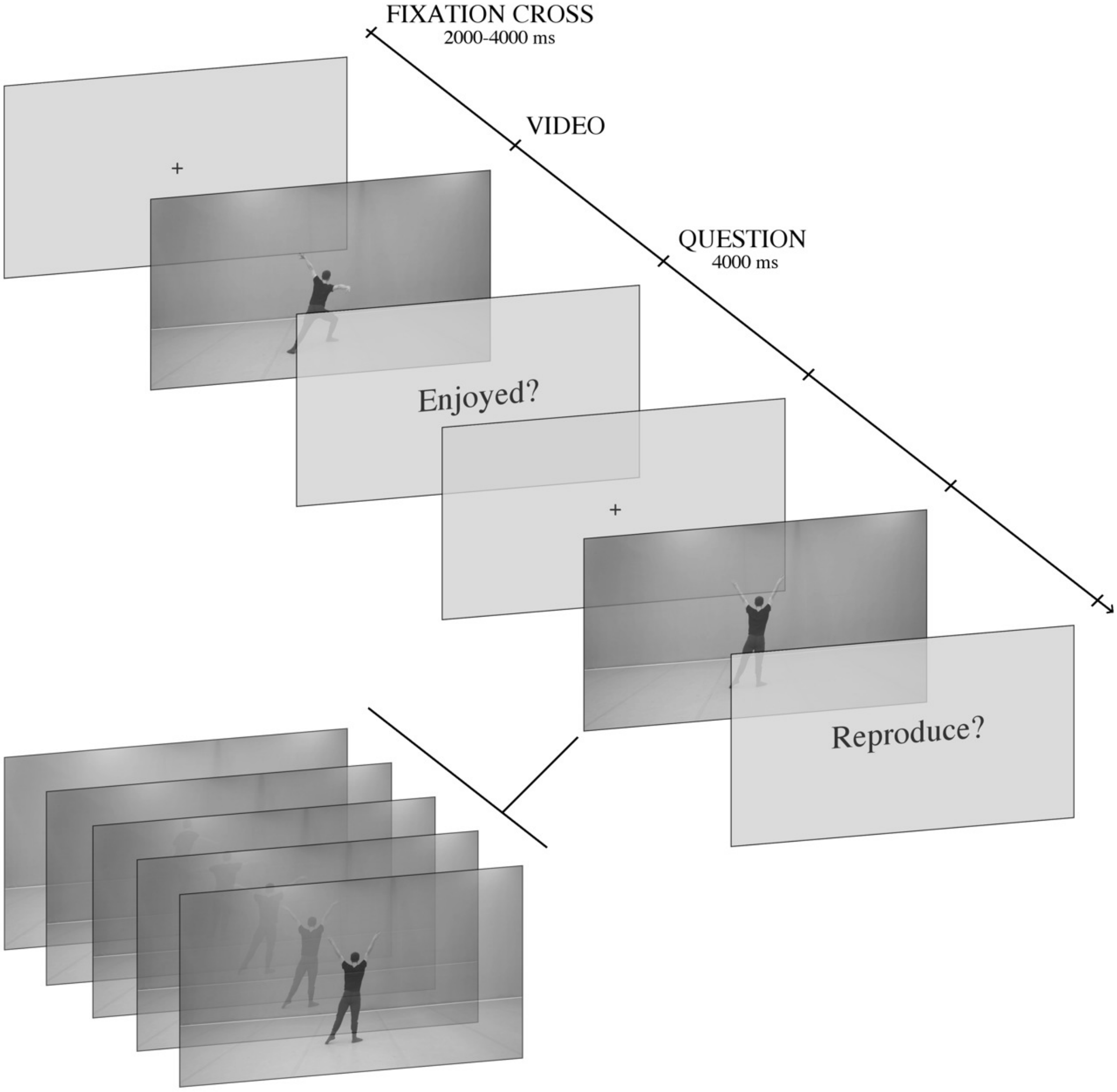


Figure 4.7. Timescale of the experimental design. Each experimental trial consisted in a counterbalanced presentation of videos depicting the uniform or varied version of dance sequences in both forward and backward playback direction. Firstly, a black fixation cross appeared on a light grey background for 2000-4000 ms. Then, a video was displayed, followed by a keyword (question) that remained on the screen for 4000 ms. The volunteers were instructed to rate each video for the perceived feasibility and enjoyability by pressing one out of four buttons on a keypad. As soon as they pressed a button, the question disappeared leaving an empty (light grey) background for the remaining time (4000 ms *minus* reaction time) until the beginning of the next trial.

4.2.5. fMRI data acquisition

All data were collected at the Centre for Cognitive Neuroimaging (CCNi) at the University of Glasgow (School of Psychology) in Scotland. Functional images were acquired on a *3-T Siemens Tim Trio MR* scanning system, equipped with a standard birdcage head coil. Functional images were acquired continuously with a single shot gradient echo-planar imaging (EPI) sequence with the following parameters: echo time TE = 30 ms, flip angle 90˚, repetition time TR = 2,000 ms. Thirty-seven axial slices allowing for full-brain coverage were acquired in ascending order (resulting in an in-plane resolution of 3 mm × 3mm, slice thickness = 4 mm, interslice gap = 10%). In addition, for each subject, a T1-weighted high-resolution anatomical scan was recorded at the end of the functional session (192 slices, 1mm thickness). The anatomical images were used to align the functional data slices with a 3D stereotaxic coordinate reference system.

4.2.6. Data Analysis

Discrimination task

Accuracy (mean of hits) in response to target videos (forward vs. backward) was recorded and measured during the discrimination task ("Direction?") that followed the main experimental task during fMRI scanning. Repeated measures ANOVA (performed using Statistica version 10 software by Statsoft) with two within-groups factors (dynamics: uniform, varied; playback: forward, backward) was performed on the mean percentage of hits.

Behavioral data

Personal ratings for feasibility and enjoyability measure were subjected to multifactorial repeated measures ANOVA with two within-groups factors, including dynamics (uniform, varied), and playback (forward, backward). A correlation between enjoyability and feasibility rating was also performed (Pearson's r).

fMRI data

Neuroimaging data from each scanning session were first analysed separately. Data were realigned and unwarped in SPM12 and normalized to the *Montreal Neurological Institute* (MNI) template with a resolution of 3 × 3 × 3 mm. This was followed by a slice timing correction, a normalization to individual T1 anatomical scans for each participant (with a resolution of 3 mm^3), and a spatially smoothing (6 mm). A design matrix was fitted for each participant, with each type of video (uniform forward, uniform backward, varied forward, varied backward), as well as fixation cross, questions + button press, and attentional control video. Due to excessive movement artifacts, the data from 4 participants were not considered for both fMRI and behavioral analysis. For the same reason, a few experimental runs from the 25 included participants were also discharged (14 out of 150 runs). Random-effects neuroimaging analyses at the group level were designed to achieve three main objectives. The first contrast evaluated the brain regions active during the observation of complex dance sequences regardless of any stimuli manipulation (video > fixation cross + questions). The second contrast evaluated the difference in neural activity during the observation of dance sequences as a function of action timing (varied > uniform moves, and uniform > varied moves). The third contrast evaluated the difference during the observation of the forward > backward movements and backward > forward movements, to investigate the impact of biological motion processing on the modulation of the AON. All neuroimaging analyses were evaluated at the whole-brain level with a voxel-wise threshold of $p < 0.001$ uncorrected and k = 10 voxels. We focus on brain regions that reached cluster-corrected significance at the FDE-cluster-corrected $p < 0.05$ level. Anatomical localization of all activations was assigned based on consultation of the Automated Anatomical Labelling Toolbox in SPM (Tzourio-Mazoyer et a., 2002).

4.3. Results

4.3.1. Discrimination task

Overall, the mean discrimination ability was 61%. ANOVA performed on the percentage of correctly categorized videos showed the main effect of the video playback factor [F(1, 24) = 13.299, $p < 0.002$]. The forward videos (67.5%, SE = 2.18%) were easier to categorize than the backward videos (54.17%, SE = 2.91%). Neither the movement dynamics factor ($p = 0.45$) nor the playback X dynamics interaction ($p = 0.29$) reached the statistical significance (see Figure 4.8).

4.3.2. Behavioral results

ANOVA performed on the reproducibility rating values showed that varied movements (1.83, SE = 0.09) were perceived as more difficult to reproduce than uniform movements (2.24, SE = 0.12), as indicated by the significant dynamics factor [F(1, 24) = 36.201, $p < 0.0001$].

ANOVA performed on the enjoyability rating values showed that varied movements (2.77, SE = 0.10) were perceived as more enjoyable to observe than uniform movements (2.33, SE = 0.09), as indicated by the significant dynamics factor [F(1, 24) = 53.630, $p < 0.0001$]. The significant playback factor [F(1, 24) = 7.190, $p < 0.02$] indicated that the forward videos (2.60, SE = 0.09) were more enjoyable to watch than the backward videos (2.51, SE = 0.09). The further dynamics X playback interaction [F(1, 24) = 5.175, $p < 0.04$] showed that only for the varied videos ($p < 0.0006$) there was a preference for the forward (2.84, SE = 0.10) than backward (2.70, SE = 0.10) playback direction, while no difference was found for the uniform videos ($p = 0.40$).

A significant negative correlation (Pearson's r) was also found between the enjoyability and feasibility ratings [r = -0.44, p < 0.0001], showing increased enjoyability with increasing perceived difficulty in reproducing the observed dance sequences.

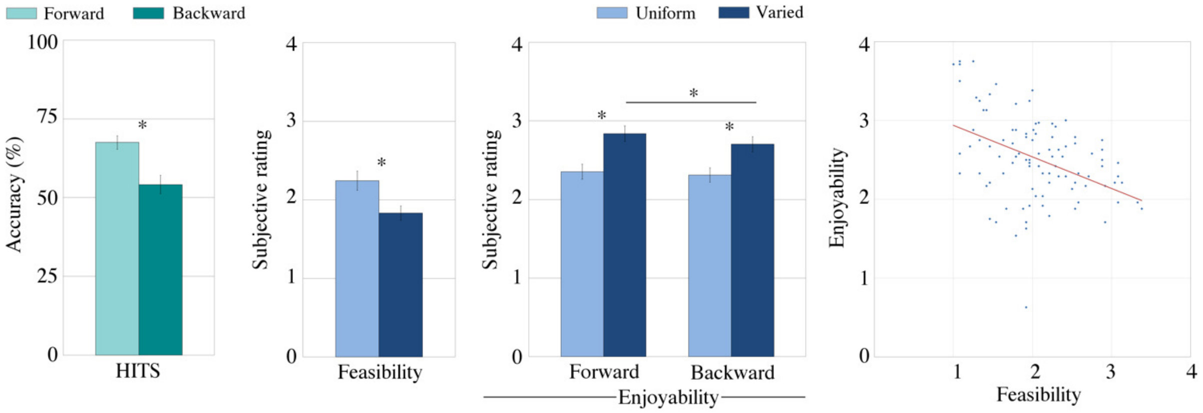


Figure 4.8. Behavioral results. The histograms (from left to right) display the percentage of accuracy in target recognition (forward vs. backward), subjecting ratings for the feasibility, and enjoyability. On the right, the scatterplot of the correlation between the feasibility and enjoyability is visible. The volunteers were more accurate in categorizing the forward than backward videos. They also rated the varied sequences (dark blue) as more difficult to reproduce and enjoyable to watch than the uniform stimuli (light blue).

4.3.3. fMRI results

Observation of dance sequences

The first imaging analysis, evaluated as all dance videos > non-videos (fixation cross + questions), showed the engagement of a broad network of brain regions consistent with the classical literature on action observation. As can be appreciated in Figure 4.9, this included the bilateral occipito-temporal cortices (BA 18, 19, 37), inferior parietal lobule (BA 40), premotor regions (BA 6) and the right superior temporal gyrus (BA 42). The full list of active brain areas can be found in Table 4.1.

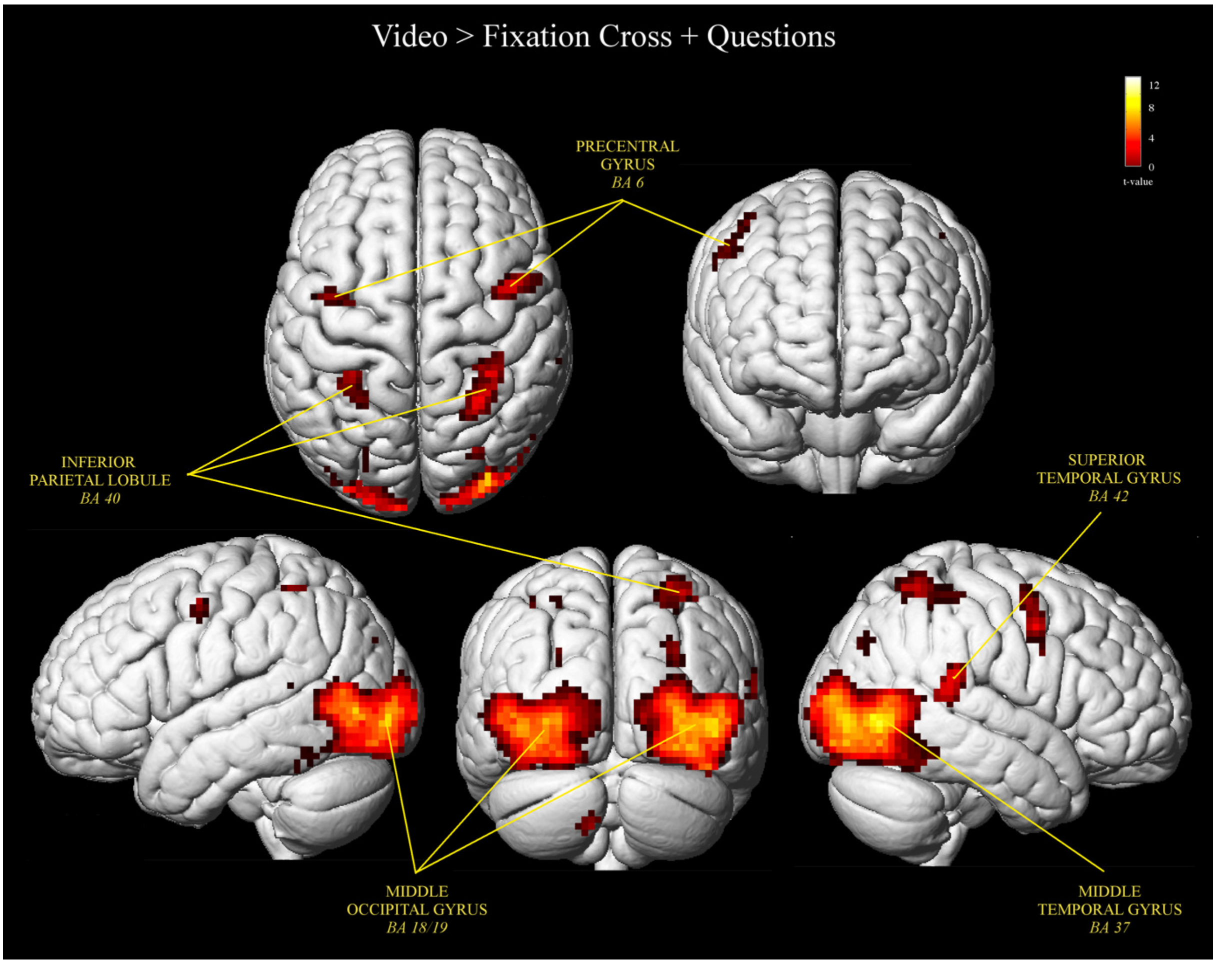


Figure 4.9. Rendering of the cortical activity related to the video observation. Main effect of video observation > non-video (fixation cross + questions). A stronger engagement of the Action Observation Network (AON) is visible, including the occipito-temporal cortex bilaterally (BA 18, 19, 37), the precentral gyri (BA 6), the inferior parietal lobule (BA 40), and the right superior temporal gyrus (BA 42).

Anatomical Regions	*BA*	*MNI Coordinates*			*T value*	*Cluster Size*	*P_{FDR} corrected*
		X	*Y*	*Z*			
R Middle Temporal Gyrus	**37**	**48**	**-70**	**-2**	**14.00**	**1242**	**< 0.0001**
R Middle Occipital Gyrus	**18**	**33**	**-88**	**4**	**12.52**		
R Inferior Occipital Gyrus	**19**	**36**	**-82**	**-2**	**12.46**		
L Middle Occipital Gyrus	**18**	**-30**	**-91**	**1**	**12.87**	**1024**	**< 0.0001**
L Middle Occipital Gyrus	**19**	**-48**	**-73**	**4**	**12.56**		
L Inferior Occipital Gyrus	**19**	**-36**	**-88**	**-8**	**11.43**		
L Inferior Parietal Lobule	**40**	**-30**	**-43**	**52**	**8.42**	**76**	**0.008**
R Thalamus		18	-28	-2	9.74	33	0.072
R Lingual Gyrus	27	6	-31	-5	4.99		
L Hippocampus	27	-18	-31	-2	8.45	17	0.208
L Cerebellum		-9	-76	-47	7.13	20	0.176
R Inferior Parietal Lobule	**40**	**33**	**-43**	**52**	**6.89**	**236**	**< 0.0001**
R Superior Parietal Lobule	**7**	**30**	**-55**	**61**	**6.70**		
R Postcentral Gyrus	**40**	**36**	**-34**	**46**	**6.67**		
R Precentral Gyrus	**6**	**48**	**2**	**43**	**6.60**	**84**	**0.006**
R Middle Frontal Gyrus	**6**	**42**	**-1**	**58**	**5.07**		
R Superior Temporal Gyrus	**42**	**60**	**-34**	**19**	**6.35**	**121**	**0.001**
R Middle Occipital Gyrus	19	30	-70	31	5.37	34	0.072
L Precentral Gyrus	6	-42	-4	49	5.30	37	0.070
L Middle Frontal Gyrus	6	-30	-7	49	4.14		
L Middle Cingulum		-15	-25	40	5.17	12	0.305

Table 4.1. List of MNI coordinates for the video observation. Locations in MNI coordinates and labels of peaks of relative activation of the regions that were more responsive to video than non-video conditions (fixation cross + questions). Results were calculated at P-uncorrected < 0.001, and k = 10 voxels. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Entries in bold denote activations significant at the FDR cluster-corrected level of P < 0.05. Abbreviations: BA = Brodmann area.

Action timing

The second imaging analysis compared the brain activity during the observation of dance sequences as a function of action timing. The varied version of the complex movements relative to the uniform version of them (evaluated as varied > uniform videos) elicited enhanced activity in a wider network, partially overlapping with that revealed by the previous contrast for video observation. As can be appreciated in Figure 4.10, this network encompassed the right occipito-temporal cortex (BA 18, 19), premotor and supplementary motor areas (BA 6), left sensorimotor (BA 2, 4), bilateral inferior frontal regions, insula (BA 44, 47, 48), and cerebellum. The full list of active brain areas can be seen in Table 4.2.

Anatomical Regions	*BA*	*MNI Coordinates X*	*Y*	*Z*	*T value*	*Cluster Size*	*P_{FDR} corrected*
R Middle Occipital Gyrus	**19**	**48**	**-76**	**1**	**9.35**	**3769**	**< 0.0001**
R Fusiform Gyrus	**19**	**36**	**-70**	**-14**	**8.13**		
R Lingual Gyrus	**18**	**15**	**-91**	**-5**	**7.96**		
R Thalamus		**18**	**-28**	**-2**	**6.14**	**320**	**< 0.0001**
R Thalamus		**6**	**-16**	**1**	**6.03**		
R Thalamus		**9**	**-25**	**1**	**5.64**		
R Precentral Gyrus	**6**	**48**	**2**	**46**	**6.08**	**131**	**0.001**
R Middle Frontal Gyrus	**6**	**42**	**-1**	**58**	**5.42**		
L Middle Cingulum		-12	-25	40	5.93	24	0.172
R Insula	**47**	**36**	**29**	**-2**	**5.62**	**63**	**0.018**
R Inferior Frontal Gyrus Orbit	**47**	**30**	**23**	**-11**	**5.02**		
L Inferior Frontal Gyrus Orbit	**47**	**-33**	**20**	**-14**	**5.29**	**169**	**< 0.0001**
L Putamen	**48**	**-24**	**14**	**1**	**4.49**		
L Insula	**48**	**-36**	**17**	**-2**	**4.03**		
L Inferior Frontal Gyrus Trian	**48**	**-39**	**17**	**22**	**5.08**	**77**	**0.010**
L Inferior Frontal Gyrus Oper	**44**	**-42**	**5**	**28**	**4.48**		
L Inferior Frontal Gyrus Trian	**48**	**-48**	**23**	**25**	**4.32**		
L Superior Occipital Gyrus	**19**	**-9**	**-79**	**40**	**4.99**	**59**	**0.020**
R Supplementary Motor Area	**6**	**12**	**2**	**55**	**4.87**	**251**	**< 0.0001**
L Supplementary Motor Area	**6**	**-6**	**-4**	**58**	**4.81**		
R Supplementary Motor Area	**6**	**6**	**2**	**61**	**4.78**		
Vermis		0	-58	-41	4.85	22	0.188
R Cerebellum		18	-58	-44	4.82	40	0.061
R Cerebellum		24	-61	-50	4.30		
L Precentral Gyrus	6	-39	-4	49	4.79	18	0.232
L Precentral Gyrus	6	-45	-4	55	3.92		
L Cerebellum		-27	-67	-50	4.75	25	0.172
L Cerebellum		-6	-31	-8	4.68	12	0.347
L Postcentral Gyrus	**2**	**-48**	**-31**	**49**	**4.48**	**62**	**0.018**
L Postcentral Gyrus	**4**	**-36**	**-22**	**52**	**4.45**		
L Precentral Gyrus	**4**	**-42**	**-25**	**64**	**3.64**		
R Precuneus	23	15	-67	31	4.14	13	0.331
L Inferior Parietal Lobule	7	-33	-55	46	4.07	18	0.232
L Inferior Frontal Gyrus Oper	48	-54	8	7	3.92	16	0.262

Table 4.2. List of MNI coordinates for the varied video. Locations in MNI coordinates and labels of peaks of relative activation of the regions that were more responsive to the varied > uniform videos. Results were calculated at P-uncorrected < 0.001, and k = 10 voxels. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Entries in bold denote activations significant at the FDR cluster-corrected level of P < 0.05. Abbreviations: BA = Brodmann area; R = right; L = left; triang = part triangularis; operc = part opercularis; orbit = part orbitalis.

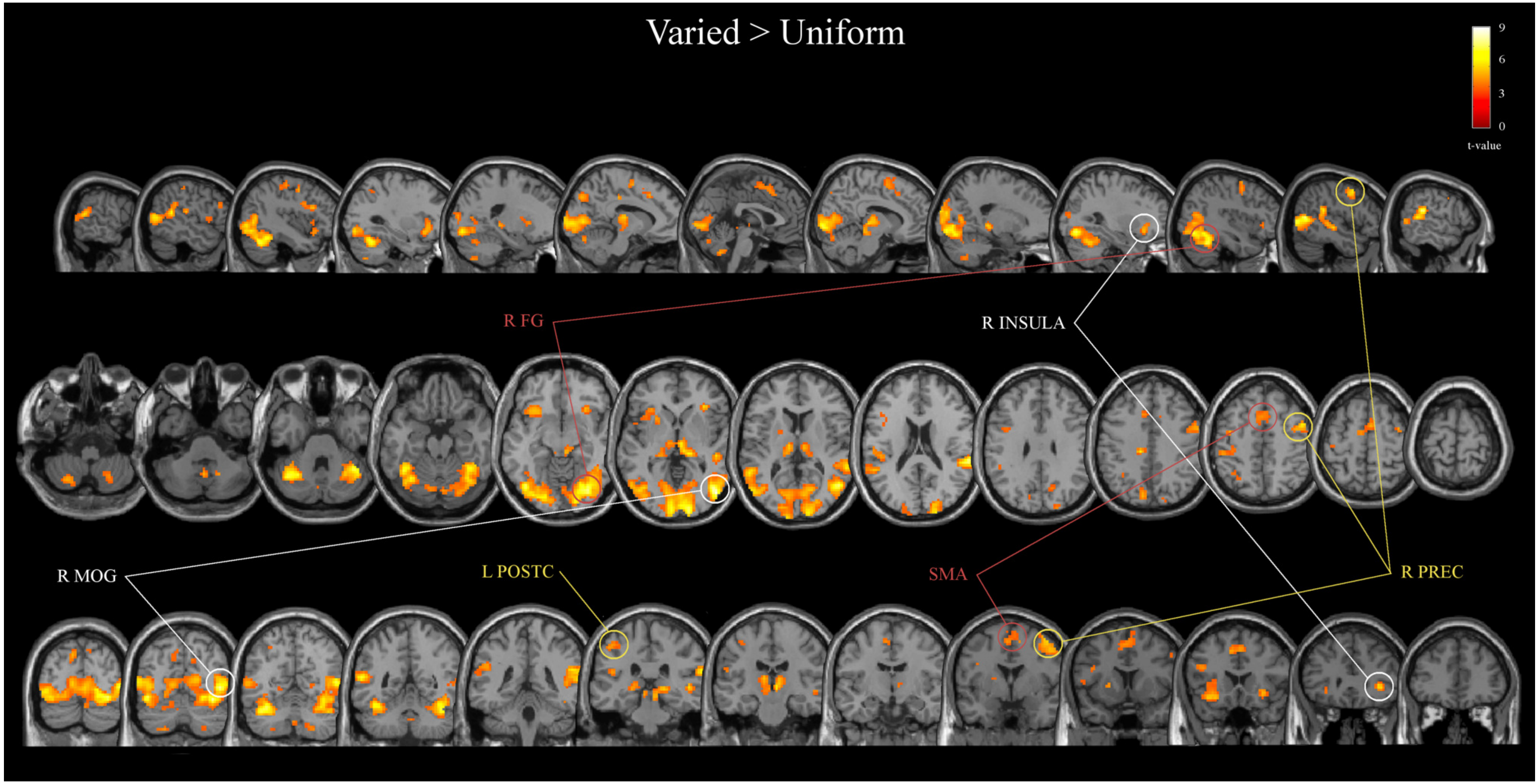


Figure 4.01. Clusters of brain activity in response to the varied videos. Each row of the figure shows thirteen brain slices in the sagittal, axial, and coronal anatomical plans. The observation of the varied > uniform videos engaged several regions within the AON, including the middle occipital gyrus (MOG), fusiform (FG), insula, supplementary motor area (SMA), precentral (PREC) and postcentral (POST) gyri.

A lower number of active regions was shown by the opposite contrast (evaluated as uniform > varied videos) when considering the FDR corrected p-values (see Table 4.3). Thus, the observation of uniform dance sequences engaged the left caudate nucleus and a few visual regions (see Figure 4.11).

Anatomical Regions	*BA*	*MNI Coordinates*			*T value*	*Cluster Size*	*P_{FDR} corrected*
		X	*Y*	*Z*			
L Caudate Nucleus		**-18**	**20**	**13**	**9.82**	**983**	**< 0.0001**
L Lingual Gyrus	**37**	**-33**	**-46**	**-2**	**9.64**		
L Caudate Nucleus		**0**	**-1**	**19**	**7.49**		
R Precuneus	**17**	**24**	**-46**	**16**	**6.69**	**88**	**0.006**
R Thalamus		**15**	**-25**	**22**	**4.06**		
R Fusiform Gyrus	37	36	-43	-2	5.87	33	0.116
R Insula	48	33	-19	22	4.59	16	0.286
R Rolandic Operculum	48	45	-13	16	3.59		
R Middle Frontal Gyrus	9	33	29	49	4.15	11	0.395
R Middle Frontal Gyrus	9	33	35	43	3.82		
R Angular Gyrus	39	51	-67	28	3.87	18	0.286

Table 4.3. List of MNI coordinates for the uniform videos. Locations in MNI coordinates and labels of peaks of relative activation of the regions that were more responsive to uniform > varied videos. Results were calculated at P-uncorrected < 0.001, and k = 10 voxels. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Entries in bold denote activations significant at the FDR cluster-corrected level of P < 0.05. Abbreviations: BA = Brodmann area.

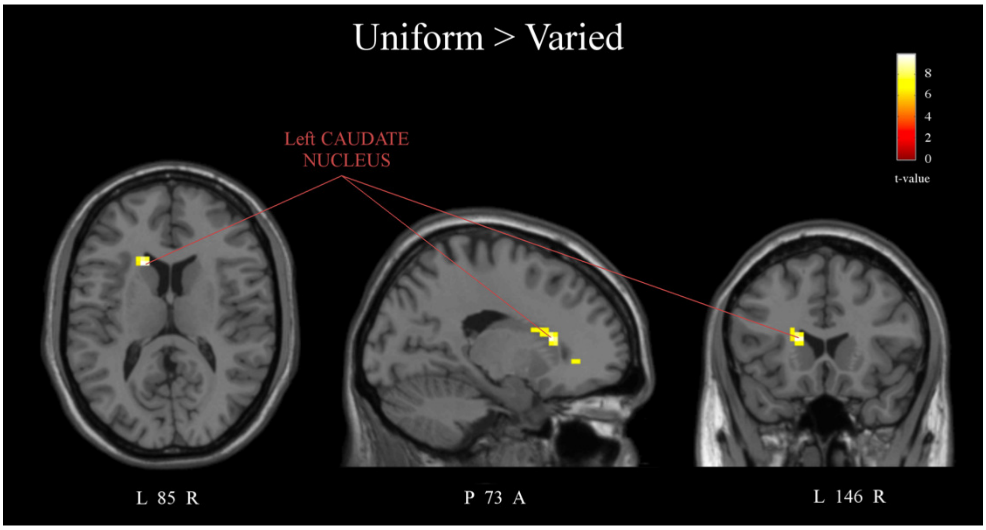


Figure 4.11. Clusters of brain activity in response to the uniform videos. The figure shows the engagement of the left caudate nucleus in response to the observation of the uniform > varied videos (P corrected < 0.05). The axial, sagittal, and coronal anatomical planes of the brain are shown.

Video playback

The third imaging analysis aimed at investigating a possible effect of the video playback on the modulation of the AON, regardless of the action dynamics. The observation of dance videos played in a natural, forward direction compared to a modified, backward direction of the same sequences (evaluated as forward > backward videos) resulted in the engagement of the bilateral occipital cortex (BA 17), including the right lingual gyrus and the left calcarine fissure (see Figure 4.12). The opposite contrast (evaluated as backward > forward videos) did not reveal any significant cluster of activity. See Table 4.4 for the full list of active brain regions.

Anatomical Regions	*BA*	*MNI Coordinates*			*T value*	*Cluster Size*	*P_{FDR} corrected*
		X	*Y*	*Z*			
L Lingual Gyrus	**17**	**-6**	**-76**	**-2**	**5.29**	**167**	**< 0.0001**
R Lingual Gyrus	**17**	**6**	**-73**	**4**	**5.23**		
L Calcarine Gyrus	**17**	**-3**	**-91**	**-2**	**3.83**		
L Superior Occipital Gyrus	17	-15	-91	10	4.67	35	0.163
L Cuneus	18	-9	-91	22	3.81		
R Thalamus		3	-7	-8	4.47	11	0.687

Table 4.4. List of MNI coordinates for the forward videos. Locations in MNI coordinates and labels of peaks of relative activation of the regions that were more responsive to the forward > backward videos. Results were calculated at P-uncorrected < 0.001, and k = 10 voxels. Up to three local maxima are listed when a cluster has multiple peaks more than 8 mm apart. Entries in bold denote activations significant at the FDR cluster-corrected level of P < 0.05. Abbreviations: BA = Brodmann area.

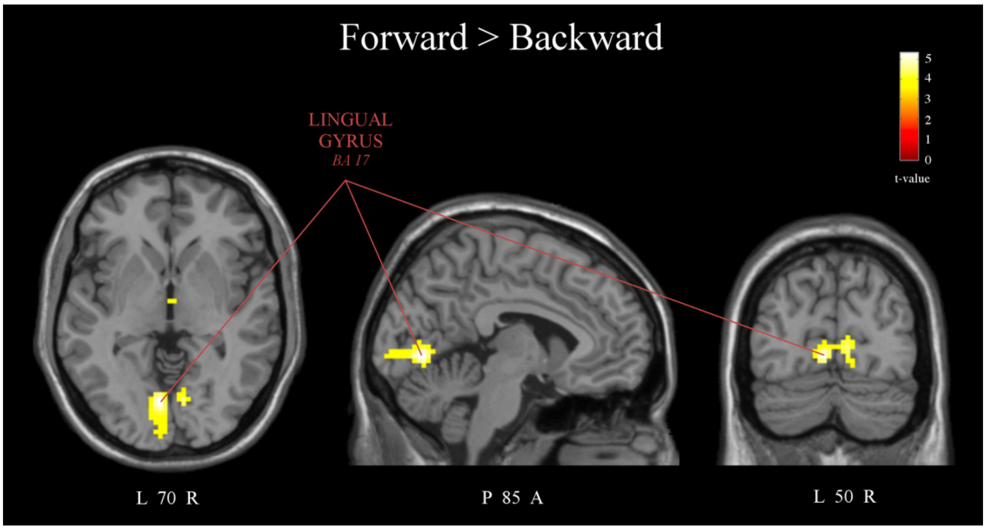


Figure 4.12. Clusters of brain activity in response to the forward videos. The figure shows the engagement of the occipital pole in response to the observation of the forward > backward videos. The axial, sagittal, and coronal anatomical planes of the brain are shown.

4.4. Discussion

The present study aimed to investigate the encoding of the acceleration in action representation during the observation of complex dance sequences. Previous evidence has shown enhanced activity in the occipito-temporal cortex, encompassing the EBA and hMT+, while observing dance movements as a function of the speed and acceleration (Noble et al., 2014; Vaessen et al., *in press*). This suggested a specific sensitivity of the EBA to perceived changes in the action timing. Fronto-central regions also seemed to have a role in the coding of acceleration of a movement, as shown by the decreased synchrony in the alpha frequency band elicited by the perception of movements characterized by high than low acceleration (Poikonen et al., 2018). However, possible confound variables (i.e., the use of the space by the dance, body part involved, type of movement) between the categories of stimuli might have had an impact the brain activity reported in those studies. Here, the brain activity of non-dancer participants was compared during the observation of contemporary dance sequences that varied only for acceleration and speed. A professional dancer reproduced the same set of dance steps in two versions, uniform acceleration or varied acceleration. Thus, the semantic content of the video stimuli remained constant (the “what” of the action) while the “how” of the action was modulated by specifically changing the timing.

First of all, the observation of all dance sequences engaged a broad network of regions in accordance with the classic literature on action observation (AON), encompassing posterior, parietal and premotor areas (Bonini et al., 2016; Hardwick et al., 2017). Regardless of the action timing and playback direction, activity was shown in the occipito-temporal cortex. A large cluster was found over the right hemisphere, overlapping with the coordinates of the EBA shown by previous authors (Downing et al., 2006), extending to the middle and inferior occipital gyri bilaterally. The activity of the EBA in static and dynamic body processing was well-established (Downing et al., 2001; Thierry et al., 2006). Relatively new findings also suggested an engagement of this region in action coding (Ma et al., 2018; Tucciarelli et al., 2015). Partially overlapping with the EBA, the hMT+ region is known to be a motion sensitive area (Ricciardi et al., 2007), generally recruited during action observation along with the STS. Here, the engagement of the right STS was consistent with extensive literature demonstrating a selective activity in the poster part of the STS in response to biological motion processing (Hirai et al., 2003; 2005; Puce and Perrett, 2003). Finally, dance observation recruited the IPL bilaterally and PM cortex, core regions of the fronto-parietal system. Several pieces of evidence reported activity in these areas during both action execution and observation (Chong et al., 2008; Culham and Valyear, 2006; Rizzolatti et al., 2002). According to the simulation theory, a visuomotor resonance process would lead to the simulation of the observed movements into the observer motor system, allowing, among others, the understanding of the action goal (Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010). A growing number of studies has been confirming the engagement of the AON during dance perception, with modulation of its activity as a function of acquired familiarity and visuomotor expertise (Calvo-Merino et al., 2015; Cross et al., 2006; 2009).

Recently, the focus of different authors moved towards the impact that the kinematic parameters of the action have on the modulation of the AON (Noble et al., 2014). In line with these studies, we found a different engagement of brain regions while observing movements that differed in time uniformity, fluency, and dynamicity. Dance sequences characterized by greater changes in acceleration (when compared with a uniform acceleration version of the same sequences) resulted in increased activity in the right occipito-temporal cortex, precentral and postcentral gyrus, SMA, and IFG/insula. The enhanced engagement of the right EBA and hMT+ within the OTC was previously reported with increasing action dynamicity of long dance sequences (Noble et al., 2014; Vaessen et al., *in press*). Here, the activity over the posterior regions included the middle (MOG) and superior occipital (SOG) gyri, extending to the fusiform (possibly including the FBA) and lingual gyri. Previously, Vaessen and colleagues (*in press*) showed a specific sensitivity of MOG and superior medial parietal cortex toward low-level features of an action, such as acceleration, magnetic moment, and symmetry. Midlevel features (i.e., lightness) were reflected by the activity of the OTC, IPL, and pSTS.

The recruitment of the motor (BA 4), premotor, and supplementary motor areas (BA 6) reported in the present investigation was consistent with the decreased alpha synchrony found by Poikonen and colleagues (2018) over posterior and fronto-central areas during the observation of movements characterized by high (than low) acceleration. Moreover, in the fMRI study by Orgs and colleagues (2016), the volunteers with sequences of 3 static images depicting body and non-body postures, ordered to produce both fluent and non-fluent apparent motion. Increased activity was found in M1 and SMA in response to fluent apparent motion sequences (body stimuli) along with enhanced functional connectivity between these regions and the right FBA. Also, activity within the SMA, pre-SMA, and PM was found during beat perception, together with the recruitment of the basal ganglia, cerebellum, STG and IFG (Grahn and Brett, 2007). In this regard, several active clusters were here found in the bilateral IFG, extending from the ventrolateral prefrontal cortex (VLPFC) to medial subcortical regions, such as the insula, thalamus, and putamen. A role of the IFG has been shown in several cognitive processes, including goal understanding during action observation (Kilner et al., 2009; Molnar-Szakacs et al., 2004), aesthetic judgment (Jacobsen et al., 2006), attentional control, and response inhibition (Hampshire et al., 2010). The activity in the insula has been previously observed during tasks requiring increased awareness, emotional processing, somatotopic mapping of body sensations (Abreu et al., 2012; Craig et al., 2009), and multimodal aesthetical appraisal (Brown et al., 2011). Furthermore, previous pieces of evidence demonstrated a specific engagement of the right VLPFC, DLPFC, and anterior insula during different time measurement tasks (Lewis and Miall, 2006). More specifically, the VLPFC and PM showed a role in subconscious motor adaptation to rhythm changes, while the DLPFC and ACC were recruited during fully conscious motor adaptation (Stephan et al., 2002).

Here, the observation of the uniform, fluent movements (compared to the varied acceleration version of them) did not lead to a modulation of the AON, as confirmed by the opposite contrast. The left caudate nucleus, lingual gyrus, and right precuneus were the only brain regions that survived the FRD correction. The caudate nucleus has been involved in several cognitive processes including rewards processing (Grahn et al., 2008), working memory (Lewis et al., 2004), goal-directed behavior learning (Sescousse et al., 2013). Activity within this region was also found during time intervals encoding (Rao et al., 2001) and other timing tasks (Grondin, 2010; Pouthas et al., 2005). For instance, it was specifically engaged during the production (tapping task) of simple metrics rather than complex metrics previously acoustically presented (Grahn and Brett, 2007). Other brain regions were active during that task condition included the putamen, palladium, STG, SMA, PM, and cerebellum. Furthermore, the caudate nucleus showed also recruitment during the aesthetic perception of artworks such as paintings (Oshin and Vinod, 2004). At the same time, activity in the precuneus has been found during action observation as a function of the motor content and the observer's strategy. An increased engagement was shown in response to meaningless compared with meaningful actions during observation for subsequent imitation rather than recognition (Decety et al., 1997). Several pieces of evidence demonstrate a role of this region in various high-order cognition processes, including self-centered imagery strategies and episodic memory retrieval (Cavanna and Trimble, 2006).

In the present study, the greater engagement of cortical and subcortical regions in response to dance movements characterized by acceleration changes might be the results of increased awareness and processing of the perceived changes in action timing. This interpretation would be consistent with evidence by an ERP study by Proverbio and colleagues (2009) on implied motion perception. The observation of images depicting dynamic/effortful actions relative to static/effortless actions elicited a larger Late Positivity component (350-600 ms in latency) over inferior frontal and centro-parietal sites of the scalp. The source reconstruction (swLORETA) estimated the neural generators of the LP in the OTC, left premotor and motor areas, STG, right ACC, and MFG bilaterally. These results were interpreted as an index of increased implied motion kinematic information conveyed by the dynamic stimuli. At the same time, other factors might have led to the present findings, including the aesthetic judgment, familiarity, and increased attention/interest toward the dance movements varied in acceleration. In this regard, our participants rated the varied sequences as more difficult to reproduce and enjoyable to watch. The significant negative correlation between these two subjective measures (r = -0,44) also confirmed that the less feasible a movement, the more interesting to observe. These results might have an impact on the modulation of the activity of several brain regions. For instance, Cross and colleagues (2011) reported a similar effect, showing that dance videos perceived as harder to reproduce were also judged more likable to watch. The conjunction analysis of these two measures revealed the bilateral engagement of the OTC and right supramarginal gyrus. Thus, in our study, the greater activity within the OTC in response to the varied movements could also be due to increased interest aroused by the variation of the temporal features.

In this regard, is not possible to exclude increased attention toward this category of stimuli, as a result of enhanced aesthetic appraisal. Previous studies have shown modulation of the activity in the IFG as a function of selective attention during action observation (Chong et al., 2008; Hampshire et al., 2010). Another factor to consider concerns the familiarity with the presented movements. An extensive literature has shown an impact of visuomotor experience on the modulation of premotor and parietal regions (Calvo-Merino et al., 2006; Cross et al., 2006). The increased activity found here in the precentral and postcentral regions might also be due to a greater familiarity with the action timing presented in the varied movements. In this regard, it is interesting to note the study by Casile and colleagues (2009). The observation of upper limbs movement violating the two-thirds power law, thus being uniform in acceleration and speed, did not lead to any significant activation. The presentation of the same movements complying with that kinematic law of motion elicited increased engagement of premotor and frontal regions. In our study, the execution of the dance steps with reduced acceleration changes might have led to a similar perturbation of the kinematic law, resulting in no specific modulation of the AON. At the same time, dance sequences characterized by greater acceleration changes might appear to be an emphasized version of normal human movements, characterized by the minimum jerk (Flash and Hogan, 1985) and time variations, thus consistently engaging the AON.

On the basis preliminary results presented here, it is not possible to disentangle the specific contribution of acceleration encoding, aesthetic preference, familiarity, and attention on the brain activity found in repose to the varied sequences. A further approach to the data might be to include the different variables at our disposal as parameters regressor in the general linear model (GLM). For instance, the scalar values of speed and acceleration computed for each video by mean of the offline motion tracking might be useful to investigate the sensitivity of specific regions to variations in action timing (Noble et al., 2014; Vaessen et al., *in press*). Similarly, a parametrical analysis using the behavioral results on the enjoyability and reproducibility ratings might highlight brain areas involved in the aesthetic appraisal of dance actions (Cross et al., 2011) as a function of perceived familiarity.

Finally, we compared the brain activity elicited by the observation of the forward and backward action. Based on previous evidence, no modulation of the early visual cortices was expected as a function of video playback, since the two class of stimuli shared the same low-level features (Hasson et al., 2008). We speculated whether difference might arise at a later stage of stimulus processing, involving, for instance, the STS, precuneus, TOJ and EBA (Maffei et al., 2015). However, when contrasting the forward direction with the inverted direction we found a cluster of activity within the bilateral occipital cortex, being specifically located in the right lingual gyrus and left calcarine fissure. No other clusters reached the significance level. Moreover, the lack of difference in the feasibility ratings anticipated the absence of differences in the modulation of any visuomotor regions. A similar pattern of results was shown by Cross and colleagues (2012) in a study where the observation of human-like actions was compared with that of robot-like actions. Regardless of the nature of the agent (a human or a robot), rigid robotic movements resulted in greater engagement of the AON, but the natural human movements (vs. robotic movements) specifically engaged the occipital pole, including the MOG and lingual gyrus.

At the same time, in this study, the observation of the backward sequences did not reveal any significant activation when compared with that of the forward sequences. The results from the discrimination task after the scanning session might partially explain the lack of effect. The ability of the participants to detect a forward video was quite high, being approximately 68%. Contrarily, their performance was just above-chance level in the backward condition (54%). Previous authors reported similar pieces of evidence showing a drop of capability when the volunteers had to categorize backward locomotor actions relative to the forward version of them. A case in point is the study by Viviani and colleagues (2011), in which videos displaying the lower part of the body of actors walking in a forward and backward direction were used as stimulus material. The authors presented the participants with the original/normal and reversed version of them in both canonical and upside-down orientation. The highest accuracy in discriminating between normal and reversed stimuli was found in the two conditions in which the actors appeared to walk forward (higher for the normal than reversed condition). The two apparent backward conditions were at the chance level and indistinguishable one from the other. Also, the upside-down presentation only slightly reduced the performance for the forward stimuli. Maffei and colleagues (2015) reported similar behavioral evidence, showing, nonetheless, increased activity in the temporo-occipital junction (TOJ) during the observation of backward movements. One possible explanation for our different findings might be ascribed to the nature of the displayed stimuli, being more complex in the case of dance sequences than locomotion. In this regard, Christensen and colleagues (2016) showed an expertise-related difference in the affective ratings of dance steps as a function of the playback direction. The dancers judged as happier the happy stimuli when presented in the forward than backward direction, while no modulation was found in the control group. This result was consistent with several pieces of evidence showing a role of acquired expertise in refining the ability of experts to process complex action details, allowing among other things the discrimination of small differences (Calvo-Merino et al., 2010; Orlandi et al., 2017) and playback direction of the steps.

In conclusion, the observation of dance sequences characterized by variations in the acceleration of the movements, relative to the same sequences reproduced with a uniform acceleration, led to a greater engagement cortical and subcortical brain regions. This network included the occipito-temporal cortex, as previously reported, but also the premotor cortex, supplementary motor areas, inferior frontal gyrus, and insula. Several factors might explain this enhanced brain activity, including enhanced acceleration encoding, visuomotor resonance processes, increased aesthetic appraisal, and attention. Further analysis would be required to disentangle the contribution of these determinants on the brain activity reported. Finally, the behavioral results indicated an increased aesthetic preference of the observers for the dynamic dance sequences, also perceived as more difficult to reproduce. These findings were in contrast with previous evidence on simple fingers and eye movements that showed a preference for reproducible and familiar actions (Beilock et al., 2007; Topolinski et al., 2010). In this regard, the motor fluency theory suggested that the knowledge of the motor program of a movement would allow a better processing during its observation (Reber et al., 2004), resulting in enhanced aesthetic preference. On the other hand, our results were consistent with those reported by Cross and colleagues (2011). The authors proposed the so-called "Cirque-du-Soleil effect" as an alternative interpretation of the relationship between perception, expertise, and aesthetic appraisal. The more complex and spectacle is an action, the more interesting and enjoyable it is to watch.

Chapter 5

General discussion

«You can observe a lot by just watching»

Yogi Berra

5.1. New insights on body and action representation

The present thesis aimed to investigate the neural processes related to body recognition and action representation. The studies presented here provide new evidence on the time course and the neural substrates of body-directed selective attention, complex action encoding, and kinesthetic motor imagery. Moreover, the brain activity of naïve viewers and dance experts was compared in one of the experiments to further investigate the impact of dance expertise in action coding. In a previous EEG/ERP study (Orlandi et al., 2017), a refined capability to automatically perceive slight differences between two almost identical novel movements was shown in expert dancers relative to non-dancer controls. More importantly, the pairs of stimuli that were used in that study varied along three main dimensions of time, space, and body shape. A similar approach was employed in a behavioral study by Henley (2015) who showed a greater ability of experts (than non-experts) in explicitly recognize pairs of movements that were matched or differed regarding time and space, but not body shape. Here, these factors were used as different tools in the three experiments to obtain new insights on action representation. Furthermore, stimuli depicting static bodies, moving bodies (single action), and sequences of complex actions were progressively employed. As a result, two experiments involving EEG and one experiment using fMRI were designed. In particular, the first study used event-related potentials (ERPs) to examine the relationship between the recognition of the human body, selective attention, and spatial orientation. In the second study, the same technique was used to investigate the role of acquired expertise with ballet in modulating the processing of technical gestures (muscular effort) during both action observation and motor imagery. The final imaging study explored the representation of action timing (i.e., acceleration) and the impact of perceived time dynamics on the activity of Action Observation Network (AON).

The first aim of the present dissertation was to investigate the effect of body orientation in recognizing the human body shape (first study). Upright and inverted images of body postures (without detail) and structures of cubes (Shepard and Metzler, 1971) were presented to the participants. The participants were instructed to categorize the stimuli by pressing a button in response to a specific category indicated at the beginning of each trial. It was hypothesized to find a modulation of the processes related to attention and stimulus categorization in response to inverted (vs. upright) bodies, but not cubes. The results revealed higher accuracy and faster reaction times, indicating that the recognition of bodies was easier compared to cubes. The ability to discriminate between categories was specifically reduced for inverted (vs. upright) body shape images, while no difference was found for images of cubes. This result is generally referred to as the body inversion effect (BIE; Reed et al., 2003; 2006).

The behavioral findings were supported by the ERP results. For body stimuli but not cubes, three ERP components were modulated by stimulus orientation . The observation of the inverted (vs. upright) body stimuli elicited a slower anterior N2 response, a larger Selection Negativity (SN) component over occipito-temporal sites (250-300 ms), and a more positive parietal P300 (350-450 ms). These results were interpreted as an index of slower stimulus processing (Batty and Taylor, 2002; Thorpe, 1996) and increased attention allocation required to recognize (Molholm et al., 2007; Proverbio et al., 2004) and categorize (Polich, 2007) the inverted body shape. As expected, no differential modulation of these components was shown for the cubes given the lack of preferential/natural orientation of this category of stimulus. Moreover, the swLORETA source reconstruction performed in the SN time window showed stronger cortical engagement in prefrontal attentional-related regions (i.e., medial and superior frontal gyri) when participants had to identify inverted compared to upright bodies. Overall, these results indicate that the recognition of the human body is strongly orientation-dependent. Moreover, these findings extend previous electrophysiological literature on body recognition that mainly focussed on the modulation of the N190 component as a function of the stimulus orientation. In those studies, the observation of inverted (vs. upright) bodies elicited a larger N190, that was interpreted as an index of a disruption of the configurational processing of the stimulus (Minnebusch et al., 2008; 2010; Stekelenburg and de Gelder, 2004).

The second study of this dissertation aimed to investigate the role of expertise in the modulation of action representation. The neuronal activity of professional ballet dancers and non-dancers was compared during the observation of technical gestures belonging to ballet repertoire. The video stimuli consisted of a series of effortful and effortless dance movements that the participants were instructed to observe and subsequently mentally reproduce (kinesthetic motor imagery). It was hypothesized to find a more refined and automatic encoding of the effort information in the experts and reduced functional asymmetry due to acquired motor knowledge. Regardless of the effort content, the observation of the dance action elicited a faster P2 component over posterior sites of the brain in experts compared to non-experts (15 ms faster). The dancers (vs. non-dancers) also exhibited a larger N2 response over the left occipito-temporal sites and a following fronto-central P300 component (360-560 ms). The source reconstruction (swLORETA) in the N2 time window showed bilateral engagement of the occipito-temporal cortex (OTC; i.e., fusiform and middle temporal gyri) and sensorimotor regions (i.e., inferior parietal lobule, superior frontal gyrus) in the ballet dancers, while the right cuneus and prefrontal regions were more active in controls. Thus, trained observers showed faster stimulus processing (Thorpe, 1996; Yang et al., 2012), enhanced recognition of the dance gesture (Jin et al., 2011; Amoruso et al., 2014), and increased hemispheric symmetry in the early OTC response. The latter result was consistent with previous evidence that showed a reduced functional asymmetry in the brain of experts whilst listening to music (Burunat et al., 2015) and note reading (Proverbio et al., 2013). This was potentially the result of plastic changes in the structures and connections of the brain due to intense and extended visuomotor practice (Jäncke, 2009; Meier et al., 2016). Furthermore, contrarily to previous evidence (Di Nota et al., 2016), it was found that dance expertise strongly modulated OTC activity during action observation.

Moreover, the comparison between effortful and effortless movements further highlighted expertise-related differences at later stages of action processing. The observation of effortful (vs. effortless) steps resulted in a more positive P300 component over anterior sites of the brain (1050-1250 ms) in experts, along with a subsequent larger parietal Late Positivity (LP) response (1400-1600 ms). The controls exhibited an enhanced LP over occipital sites only as a function of increased effort. The source reconstruction (swLORETA) in the LP time window showed the recruitment of visuomotor regions in experts (i.e., inferior parietal lobule) and prefrontal and visual regions in controls (i.e., superior and inferior frontal gyri, middle and inferior temporal gyri). These results likely indicate a refined ability to encode effort information in dancers due to their acquired motor knowledge of the steps (Aglioti et al., 2007; Mangels et al., 2001). At the same time, working memory processes were possibly required by the controls to process the increased amount of kinematics conveyed by the effortful stimuli (Sitnikova et al., 2003; 2008). Thus, the encoding of muscular effort seemed to rely on the activity of visuomotor regions and not the mentalizing system (Mizuguchi et al., 2016). This was consistent with increased autonomic functions and corticospinal excitability shown in previous studies (Alaerts et al., 2010a; 2010b; Paccalin et al., 2000).

The different action coding based on expertise could also be observed during the mental simulation of the observed gesture. A larger Anterior Negativity (AN) component (400-550 ms) was found in the dancers compared to non-dancers, which was also differentially modulated by the motor content of the imagery. The AN (Cebolla et al., 2015) was enhanced during the motor imagery of effortful (vs. effortless) steps in controls, but not experts. The reconstruction of the source (swLORETA) performed on the difference wave (effortful-*minus*-effortless) in the AN time window highlighted a stronger engagement of inferior and middle temporal regions in dancers (Wei and Lou, 2010) together with more bilateral recruitment of visuomotor regions (Hétu et al., 2013). This was likely the result of a more refined recall of body-related and sensorimotor information relative to the effortless stimuli. Contrarily, the superior and medial frontal areas were mainly activated in non-dancers (Abreu et al., 2012), suggesting an increased cognitive load required to imagine effortful movement due to a lack of motor knowledge.

In the light of these results, it is important to consider an fMRI study by Pau and colleagues (2013), in which the brain activity of expert and non-expert musicians was compared during the observation and execution of finger movements during piano playing. Pau et al. (2013) found an enhanced engagement of visuomotor regions in the musicians (vs. controls) during the observation/learning phase of the study. Contrarily, similar brain regions were activated more strongly in controls during the real execution of the same sequences of movement. These results were interpreted as an index of "neural efficiency", by which the experts were able to better codify the action due to acquired motor knowledge and, consequently, they required less neural resources during the execution. In the present thesis, the encoding of effortful (vs. effortless) movements required increased neural activity in the dancers, as indexed by the larger frontal P300 and parietal LP components. Therefore, it is possible that the reduced AN response found during the subsequent motor imagery of the same steps was the results of the previous deeper action processing. Further studies will be required to clarify the modulation of motor imagery processes as a function of expertise and motor content. For instance, this would include the exploration of the impact of the visuomotor expertise on attentional and mnemonical capacities. Altogether, results from the second to study of this thesis reveal a significant impact of dance expertise on action representation, reflected during both observation and mental simulation in the trained participants.

The last study of this thesis aimed to investigate the representation of action timing and the role of perceived time dynamics (i.e., acceleration and speed) in modulating the activity of the AON. Participants were presented with the forward and backward version of videos depicting complex dance sequences reproduced in a uniform or varied way based on the acceleration of the movements. They were instructed to rate their aesthetic preference at the end of each clip. We speculated to find a greater engagement of occipito-temporal and fronto-central regions in response to the dance videos characterized by greater changes in the acceleration (compared to uniform acceleration). From a behavioral perspective, the movements varied in acceleration (vs. uniform) were perceived as more enjoyable to watch but more difficult to reproduce. Moreover, the direct comparison of the brain activity during the observation of varied vs. uniform sequences showed the engagement of a broad network encompassing cortical and subcortical regions. This included the occipito-temporal cortex, premotor and supplementary motor areas, inferior parietal lobule, inferior frontal gyrus, insula, thalamus, and putamen. According to previous evidence, strong modulation of the extrastriate body area (part of the OTC) was found as a function of acceleration profile of the action (Noble et al., 2014; Vaessen et al., *in press*). More importantly, a role of the visuomotor and subcortical regions (Grahn and Brett, 2007; Lewis and Miall, 2006) was found in the processing of time variations during action observation. This suggests a strong embodied response during the processing of action timing reflected by a variation in the kinematics of the movements. Increased attention, familiarity, and aesthetic pleasure might have a role in the enhanced brain activity reported here. Further analysis would be required to disentangle the contribution of these different factors, including parametrical analyses using speed and acceleration measures, as well as behavioral ratings as parametrical regressors. The employment of more advanced data analysis techniques (i.e., MVPA) might also be relevant to identify more accurately the specific contribution of each brain region in action processing.

In conclusion, the evidence reported in the present thesis is consistent with the hypothesis of an impairment of body-related (Stekelenburg and de Gelder, 2004) and not face-related (Brandman and Yovel, 2010) configurational processing underlying the body inversion effect (BIE). In this regard, the stimuli used in our first study were wooden dummies that represented the human body shape without any facial or body detail. Thus, no face recognition process could have modulated the BIE. The features of the stimuli also avoided any possible artifact caused by face blurring or head removal (Munnebusch et al., 2008) in the images of the bodies. Furthermore, our results support the hypothesis that the visual processing of an inverted body is more demanding relative to an upright body (Reed et al., 2003; 2006), as shown at both behavioral and neural level. In our investigation, the increased SN, P300, and slower N2 response elicited by the observation of the inverted body represent novel findings in the study of body processing. The modulation of these components seems to suggest enhanced attentive selection required to process and categorize a body displayed in a non-canonical orientation. Hence, these pieces of evidence indicate that the recognition of the human body is critically dependent on its orientation. An outstanding issue concerns the reason for the faster and less demanding perception of the upright (compared with the inverted) body. Further studies will be required to disentangle the contribution of a possible innate bias for an orientation-dependent biological predisposition in body processing (Bardi et al., 2014; Simion et al., 2008) from that due to perceptual expertise acquired over time. An example in this regard is the comparison between stimuli depicting body postures and real objects with whom participants have high visual familiarity, during a categorization task. Previous authors (Stekelenburg and de Gelder, 2004; Reed et al., 2006; Zhou et al., 2010) have used the objects (i.e., houses, shoes) as a control condition for the body and have shown no impact of the object orientation on RTs or early neural response (N190 component). However, a possible modulation (or a lack of modulation) of the ERP components reported in our study in response to the inverted (relative to upright) object would be useful to clarify the role of visual expertise in the inversion effect. Also, participants who have been training for hours in non-canonical positions (i.e., acrobats, trapeze artists) could likely have acquired specific expertise with inverted bodies. A comparison between this category of experts and non-expert controls during a recognition task will help to investigate this point.

As regards the neural representation of action, the results obtained and presented in this dissertation are consistent with previous significant theories. This includes the concept of action topography, the simulation hypothesis, and the "neural efficiency" theory. Firstly, we found that the encoding of the motor content (i.e., muscular effort and acceleration) of whole-body complex action was not limited to a specific brain region. It required the engagement of a broad network encompassing fronto-temporo-parietal areas (Grafton and Hamilton, 2007; Rizzolatti et al., 2001), generally referred to as the Action Observation Network (AON). Specifically, the coding of both muscular effort and acceleration information resulted in the activity of prefrontal and occipito-temporal areas. The processing of effort-related action kinematics also required the activity of superior parietal and temporal regions (i.e., IPL, STG). The acceleration-related action kinematics elicited activity in the ventrolateral prefrontal cortex (i.e., IFG) and medial subcortical regions (i.e., insula, thalamus, and putamen). These results show either a common neural substrate engaged by action encoding but also specific sensitivity of different brain regions to various action features (Handjaras et al., 2015; Ricciardi et al., 2013). The differential modulation of the AON reported in the two studies can be certainly ascribed to several further factors. This includes, for instance, the experimental task (and technique used), the relative requirement of attentional resources, and the stimuli employed (i.e., single dance steps vs. long sequences of dance movements). In this regard, the ERP study required the recognition of the dance gesture to mentally simulate it, while an aesthetic judgment task was requested during the fMRI investigation.

Furthermore, in the present study, a pivotal role of the occipito-temporal cortex (OTC) in action representation was shown during both observation and imagination (Guillot et al., 2009; Tucciarelli et al., 2015). The activity of the OTC was also strongly modulated as a function of the participants' expertise with the observed movements. Previous evidence has shown an enhanced involvement of the OTC during the observation relative to the imagery of repertoire specific movements (Di Nota et al., 2016; Wei and Luo, 2010). Moreover, in those studies, the direct comparison between experts and non-expert controls did not reveal any significant group-related difference during both imagery and observation. Contrarily, we found here a more bilateral engagement of the OTC in the early stage of action processing in dancers compared with controls. Then, greater activity in the OTC during effort encoding (observation phase) was shown in controls (compared with dancers), while enhanced activity in the imagery task was found in dancers (compared with controls). The different task proposed (i.e., passive vs. active observation) to the participants and the complexity of the action used (i.e., technical movements vs. repetitive movements) are factors that might partially explain the reason why the previous authors have not shown an OTC modulation based on expertise. Overall, our findings point out a specific involvement of the occipito-temporal regions in action representation and specifically in motor imagery. More importantly, the contribution of these cortical areas is strongly modulated as a function acquired expertise.

Several brain regions showed also to be differently engaged based on the motor knowledge of the observers in our studies, including the fronto-parietal areas. According to the simulation hypothesis (Rizzolatti and Craighero, 2004), the observation of a known action results in a recall of the motor program required by the actual action execution. Several pieces of evidence have shown that increased visuomotor expertise with the repertoire of movement leads to an enhanced activity of premotor (i.e., vPM; SMA) and parietal (i.e., IPL) regions (Abreu et al., 2012; Aglioti et al., 2008; Babiloni et al., 2008). Consistently with these studies, we found enhanced engagement of these areas in dancers relative to controls as a result of extensive training. The expert dancers were likely able to recall the motor program of the trained actions and to simulate the movement while observing it or imagining it. At the same time, increased cognitive load and attentional resources was likely required to complete the tasks by the observers lacking in motor knowledge. A similar interpretation might also partially account for the greater activity in premotor regions elicited by the observation of varied (compared with uniform) videos in the fMRI study. Human actions are characterized by various time variations and minimum jerk (Flash and Hogan, 1985). The varied stimuli might have appeared as an emphasized version of normal human movements. Thus, the participants might have been able to simulate more easily the movements that varied in time dynamic due to a greater familiarity with this category of action.

Our evidence is also consistent with the so-called "neural efficiency" theory. Previous findings have shown a more refined specialization of brain circuits as a result of extensive motor training (Babiloni et al., 2010; Pau et al., 2013). According to these studies, we reported a deeper coding of effortful (compared with effortless) movements in experts during action observation (larger frontal P300 and parietal LP). This resulted in decreased neural resources required by the subsequent motor imagery of the same category of movement (relative to effortless movements), as indexed by the smaller AN response. A similar result was previously reported for action observation and subsequent real execution in professional piano players (Pau et al., 2013). This evidence is consistent with the idea of functional similarity between motor imagery and action preparation processes proposed by several authors (Jannerod, 1994; 2001; Ruffino et al., 2017). Another example of increased efficiency is the enhanced functional symmetry found here in the early OTC response (larger N2) in dancers relative to controls. Faster processing of the moving body (faster P2) was also shown in the expert participants. These ERPs modulation can be likely interpreted as an index of a more efficient body- and movement-related processing as a result of the extensive professional practice (Burunat et al., 2015; Proverbio et al., 2013).

Overall, these pieces of evidence show that brain processes underlying action representation can be modulated by several factors, including the experimental task, attentive resources, and motor content of the action. Also, the manipulation of the expertise with the specific action can be used as a tool to investigate complex action processing. It can bring out specific changes in brain activity as a function of motor knowledge and familiarity. These elements have to be thoroughly taken into account in creating new models and experiments to investigate and conceptualize action representation processes.

In this regard, whether the brain activity of expert and non-expert dancers was compared in the study on muscular effort encoding, the other two studies involved participants without any specific expertise. The inclusion of a group of professional dancers (along with controls) in the investigations on the body inversion effect and acceleration encoding could represent a valuable development of the present thesis. This could provide useful insights into the capability to mentally rotate the body in the space (Jola and Mast, 2005) or to perceive changes in the rhythm of an action (Leman and Naveda, 2010) as a function of acquired expertise. In this regard, the extensive training allows the dancers to rotate the body in the space without losing the spatial reference (Nigmatullina et al., 2013). One might expect reduced attentional allocation required to recognize a body when presented in an unnatural orientation. Moreover, the dancers exhibited refined coordination and motor control during the execution of a whole-body movement (Krasnow, 2011). Precise synchrony with the music tempo or between dancers is also required from professional dancers during a performance (Miura et al., 2011). This might lead to a more selective recruitment of brain regions sensitive to action timing. If found, such results would also strengthen the present finding from the second study; i.e., faster processing of the moving body and enhanced functional symmetry in experts (than non-experts) as a result of intense dance training.

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