Neurobiological bases of multimodal visuo-somatomotor interaction in human movement

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Specific Aims of this Dissertation

In this thesis, I investigate the neural mechanisms underlying sensorimotor integration in healthy subjects through both electrophysiological and neuroimaging experiments. This objective will be pursued by investigating, first, the brain mechanisms underlying the execution of actions varying in complexity, and second, by exploring the neural mechanisms underlying the execution of a cognitive-motor dual-task during real or simulated locomotion. The general goal is to clarify how the brain integrates multimodal sensory information—including visual, vestibular, and proprioceptive cues—with cognitive processes to support adaptive motor behavior.

In Chapter 1, I will introduce the general **theoretical and evolutionary framework** that constitutes the conceptual foundation of the entire dissertation and of all the experimental works conducted during my Ph.D. Specifically, I will outline the evidence supporting the **intrinsic and reciprocal relationship between movement and cognition**, emphasizing how complex cognitive functions have progressively evolved from neural systems originally dedicated to motor control. Through the integration of neuroanatomical, neurophysiological, and evolutionary perspectives, I will describe how shared cortical and subcortical networks—particularly involving cerebellar, basal ganglia, parietal, and prefrontal circuits—underpin both cognitive and motor operations. Special attention will be devoted to the evolutionary transition to bipedalism, which profoundly shaped human brain organization, promoting the development of executive and integrative functions necessary for adaptive interaction with the environment. This chapter therefore provides the overarching theoretical framework within which all subsequent chapters and experimental studies are conceptually grounded, defining the unifying perspective from which the neural bases of **sensorimotor and cognitive integration** are investigated throughout this thesis.

In **Chapter 2**, I will present first a review of neurofunctional studies first about **motor complexity**, outlining how different levels of movement complexity have been defined and investigated across **behavioral, electrophysiological, and neuroimaging approaches**. I will describe the brain mechanisms underlying the execution of actions varying in complexity, to assess how the complexity of the motor response modulates the different cognitive resource allocation strategies and functional interactions between areas involved in motor coordination and in the high-load cognitive tasks execution. This was aimed at defining a key theoretical framework for the **first and second studies** of my Ph.D. on the modulation of brain activity as a function of action complexity presented in **Chapter 6 and 7** of this thesis.

In **Chapter 3**, I will provide a **detailed description of the Dual-Task paradigms** which represent an ideal framework to investigate the interaction between cognitive and motor processes under conditions of shared resource allocation**.** I will provide a detailed description of the Dual-Task paradigms, illustrating their theoretical foundations, methodological variants, and main neurophysiological evidence from both I will describe the principal theoretical models that have been proposed to explain dual-task effects—namely the limited-capacity, interference-based, facilitation-based, and dynamic resource-sharing models—highlighting how each accounts for performance modulation and neural correlates under concurrent task execution. Furthermore, I will discuss how dual-task paradigms have been adapted to study locomotion and postural control, with special emphasis on ecological walking conditions and their impact on attentional load, executive control, and sensorimotor integration. This was aimed at defining a key theoretical framework for the third and fourth studies of my Ph.D. on the effects of walking on brain processing during a concurrent cognitive task presented in Chapter **6**,**7, 8 and 9** of this thesis.

In **Chapter 4,** I will present **a review of neurofunctional studies** in monkeys and humans about the integration of signals from different sensory modalities occurring in visual and somatomotor cortical regions in order to visually guided the locomotion. In the first section of the chapter, I will examine the close interplay between motor and cognitive functions, highlighting evidence that these systems are evolutionarily and functionally interdependent, sharing neural resources that allow for efficient information integration during movement. In the second section of the chapter, I will provide a comprehensive overview of both visual and somatomotor cortical regions traditionally associated with egomotion processing in both monkeys and humans. In the third part, I will combine evidence from the human brain to suggest the possible functional role played by these cortical regions. In addition, I will discuss the functional models that clarify how these areas interact with each other during the processing of retinal visual information and proprioceptive signals to plan and control limb movements during actions. This was aimed at **defining a key theoretical framework for the functional Magnetic Resonance Imaging (fMRI) studies** of my Ph.D. **on** the neural underpinnings of visually-guided of complex motor actions presented in chapter x of the present thesis.**This framework will serve also as the basis for discussing cognitive-motor dual-task theories, particularly in relation to how both real and simulated locomotion modulate visual discrimination tasks performance.**

In **Chapter 5**, I will provide a **detailed description of the EEG system** and of the equipment used to carry out the research described in the following chapters, as well as of the materials, methods, and procedures employed. Particular attention will be given to the **cognitive-motor task that** was used to investigate the dynamics underlying the performance of the dual-task. Furthermore, I will provide an overview of the main ERP components – preparatory and elaborative – investigated, focusing on their role in locomotion, as well as in the sensorimotor integration necessary for the performance in complex tasks and on the way in which they are connected to one another and interact with each other, allowing for an efficient and adaptive allocation of cognitive and motor resources. The aim will be to discuss how these components are shaped by the interaction between cognitive demands and motor activity, and what they reveal about the temporal dynamics of sensorimotor integration.

In **Chapter 6,** I will present my first EEG study on **preparatory brain activity preceding visually guided actions of different motor complexity** using a visuomotor discrimination task. Unlike prior work focused on simple, single-effector actions, this study examined preparation for more complex movements involving both upper and lower limbs, including whole-body coordination during stepping. Event-related potential (ERP) analyses revealed distinct temporal and cortical patterns: simple responses showed early premotor activation with strong prefrontal control, reaching movements engaged parietal regions, and stepping involved bilateral dorsomedial parieto-occipital areas linked to sensorimotor integration and environmental anticipation. These findings highlight how the brain dynamically recruits specialized preparatory mechanisms according to action complexity, supporting the view that sensorimotor and cognitive systems are integrated even before execution. The novelty of this study lies in its focus on preparatory brain activity, as crucial as online control.

In **Chapter 7**, I will present the second study examining how **cognitive processing interacts with motor demands** under increasing action complexity. While previous work showed that complex actions recruit broader sensorimotor networks, less is known about their impact on concurrent cognitive processes during tasks requiring both perceptual discrimination and motor response. Using a visual discrimination task (DRT), I tested whether motor response complexity modulates ERP indices of perception, attention, and decision-making. Results revealed that as motor demands increased, resource distribution shifted: early perceptual and attentional ERPs (P1, N1) were enhanced, whereas the P3—linked to higher-order cognitive control—was reduced, reflecting a trade-off favoring motor execution. Additionally, a late negative component (N750), associated with response selection, increased with motor complexity, underscoring greater neural investment in action planning. Importantly, accuracy remained stable, showing that the brain reallocates resources dynamically to preserve performance. Unlike prior studies, this research incorporated whole-body actions such as stepping, an ecologically valid and frequent daily movement, making it ideal for probing sensory, cognitive, and motor integration. Overall, the findings support a "motor-priority" model, where motor demands are prioritized at the cost of late-stage cognitive resources.

In **Chapter 8**, I will present the third study on the **anticipatory brain dynamics associated with locomotion under ecological sensory stimulation**. This study focused on preparatory ERP components (BP and pN) during a visual discrimination task while participants were either standing still or walking, with and without optic flow. Results showed that walking enhanced both motor and cognitive preparation, improving response speed and accuracy. The presence of optic flow further amplified motor readiness but simultaneously impaired cognitive preparation and accuracy, demonstrating its dual role as a factor increasing ecological validity while also introducing sensory competition. The design—contrasting stationary and walking conditions with or without optic flow—was particularly suited to investigate the mismatch effect, highlighting how perceptual-visual and somato-motor signals dynamically interact in modulating the allocation of cognitive resources during preparation.

In **Chapter 9**, I will present the fourth study on post-stimulus ERP components, examining the **temporal unfolding of perceptual and decisional processes under** the same **dual-task** conditions. Walking was found to enhance attentional processing (N1) and sensorimotor integration (pP1), while optic flow modulated early visual processing (P1) and increased attentional demands, leading to reduced accuracy. Importantly, optic flow did not affect late cognitive evaluation (P3), but early ERP modulations suggested a redistribution of cognitive resources under multisensory load. These findings provide strong neurophysiological support for the multiple resource theory, showing that walking—particularly when combined with naturalistic visual stimulation—reshapes the balance between preparatory and online processing. This underscores how cognitive and motor systems flexibly interact in real time to ensure efficient performance and a functional adaptation to the surrounding environment.

Together, all these studies advance our understanding of how the brain balances cognitive and motor demands during complex, ecologically valid actions, highlighting the flexible allocation of neural resources necessary for effective perception and action in dynamic environments. In sum, this research offers novel neurophysiological insights into the flexible and dynamic nature of cognitive-motor integration. By combining traditional EEG approaches with ecologically valid movement paradigms, it contributes to a more nuanced understanding of how the brain manages simultaneous perceptual, cognitive, and motor demands in real-world scenarios. These insights have implications not only for basic neuroscience but also for applied domains such as rehabilitation, human-machine interaction, and sports science, where optimizing the coordination of cognition and movement is of central importance.

Scientific Production of BiancaMaria Di Bello

Publications

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Poster Presentations

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Abstracts

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Theoretical Part

1. Introduction

1.1. Interconnection between Movement and Cognition: Neuroanatomical and Functional Foundations

Numerous neuroscientific findings support the idea that movement and cognition are functions that are closely interconnected, not only functionally but also structurally. Cortical and subcortical areas involved in the execution and planning of movement (such as the cerebellum, basal ganglia, premotor and prefrontal cortex) are also implicated in higher cognitive processes, such as attention, working memory, planning, and cognitive flexibility. This theory is strongly supported by Leisman et al. (2016), who argue that complex cognitive functions such as planning, attention, language, and executive control did not develop "from scratch," but rather evolved from neural circuits originally dedicated to motor control. In other words, the brain mechanisms that initially served to plan, control, and regulate bodily movement have been reused, expanded, and adapted over the course of evolution for more abstract cognitive purposes. This occurred particularly thanks to the expansion of the connections between the motor cortex, responsible for voluntary movement control, and the prefrontal areas, which are involved in higher cognitive functions. This hypothesis is supported by research attributing to the cerebellum—not only traditionally associated with mere motor coordination, balance, and postural control—cognitive and linguistic processes. In fact, specific areas of the cerebellum are activated in linguistic tasks, working memory, attention, and regulation (for a review see Stoodley & Schmahmann, 2009).

A similar hypothesis was advanced by Llinás (2001), who proposes a unified view of brain functions, emphasizing that the brain originally evolved for movement, and that cognitive functions emerged as sophisticated elaborations of these same systems. According to this theory, movement is functional for interacting with the environment for the purpose of survival, and the motor brain structures were therefore the first to develop. Subsequently, the need to coordinate and regulate movement through the generation of internal models to anticipate and plan actions led to the evolution of neural systems. From this perspective, perception itself is subordinate to movement: sensory information is not an end in itself but is useful to guide behavior and optimize motor interactions with the environment. The brain is therefore not passively dedicated to receiving sensory information but is configured as an active predictive system. Cognitive functions such as attention, memory, or planning would be internal tools functional to prepare and optimize action. Llinás proposes that many higher cognitive functions, such as abstract thinking, language, or self-awareness, evolved from increasingly complex motor control mechanisms. Brain structures involved in movement, such as the cerebellum, basal ganglia, and motor cortex, are closely interconnected with cognitive areas such as the prefrontal cortex. This is demonstrated by the fact that mental simulation of movement—that is, imagining or planning an action before executing it—is at the basis of many cognitive functions such as problem-solving or symbolic thinking.

Since the brain areas that control fine hand movement are closely connected to those involved in language and thought, Rizzolatti & Arbib (1998) proposed a theory called the "Mirror System Hypothesis," according to which motor and premotor areas, originally developed for object manipulation and for observing others' actions, have been evolutionarily reused for language. In fact, the mirror neuron system is activated both when an action is performed and when one observes another performing it. This mechanism would underlie a continuum—a process that progressively led to the development of imitation, gestural communication, and eventually verbal language. Manual gestures were likely the first form of intentional communication between individuals (gestural proto-language). These gestures required an internal representation of the action, the ability to anticipate its effects, and to imitate. With evolution, the motor circuits involved in gestures would have been reused to produce vocal gestures and eventually for articulated language. This process would have involved the premotor area and subsequently Broca's area, originally involved in the motor coordination of the hand. The mirror neuron system in humans is located precisely in the premotor areas and in Broca's area. This suggests that understanding others' actions and understanding a linguistic message share the same neural circuits. This would suggest that language did not arise as an "abstract function" but as a neural extension of the ability to represent and understand actions. Evidence for the involvement of areas responsible for verbal language analysis and production in motor functions derives from the observation that patients with lesions in Broca's area show difficulties not only in language but also in producing complex motor sequences (ideomotor apraxia) (Goldenberg, 1995; Heilman, Rothi, & Valenstein, 1982). Moreover, during language comprehension, Broca's area is activated even in the absence of verbal production, suggesting a role in meaning comprehension through action models (Pulvermüller et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti et al., 2005).

Finally, based on neurophysiological and behavioral data, Mendoza & Merchant (2014) suggest a shared neural basis between temporal control of movement, time perception, and numerical cognition. Temporal motor control represents the brain's ability to plan, initiate, and regulate movements precisely over time. The same brain areas (such as the basal ganglia, premotor cortex, and cerebellum) are involved both in motor timing and in cognitive tasks related to time (e.g., judging the duration of a stimulus) and numerical estimation (e.g., counting, estimating quantity). Furthermore, neurons that encode duration or rhythm are activated both in movement and in abstract cognition. Therefore, movement, time perception, and numerical cognition are not separate systems but intertwined functions that share common neural networks. This offers an explanation for the fact that motor experience can positively influence abstract cognitive abilities.

The link between movement and cognition is further supported by studies showing that regular physical activity can induce neuroplasticity and neurogenesis, especially at the level of the hippocampus and prefrontal cortex. For example, physical activity increases the production of BDNF (Brain-Derived Neurotrophic Factor), a protein that promotes the survival and growth of neurons, improving learning and memory (Cotman et al., 2007).

1.2. Common Evolutionary Origins and the Role of Bipedalism in Brain Development

The theory according to which cognition and movement share a common evolutionary origin is also based on the observation that animals with more complex motor abilities tend to have more developed brains. In particular, the evolution of human bipedalism would have had a significant impact on brain reorganization (**Fig.1**). Harcourt-Smith (2010) emphasizes how the transition to upright posture and bipedal locomotion required greater fine motor control, anticipation, and coordination, thus stimulating the development of more complex brain networks. This adaptation freed the upper limbs for tool use, contributing to a greater specialization of the hands and to the development of cortical areas responsible for fine motor control and manipulation, which are also closely linked to cognitive and linguistic functions (Rizzolatti & Arbib, 1998). Among these are the primary motor area (M1), particularly the part that controls the fingers and hands; the premotor area and the parietal cortex, which integrate vision, touch, and movement; and the associative cortex, which is fundamental for planning, observing, and imitating complex actions. Moreover, with the evolution of bipedalism, a gradual process of “encephalization” is observed, that is, the increase in brain volume and the consequent brain/body ratio (Holloway, 1996; Falk, 2007). The primary motor and premotor areas expanded to integrate the control of bipedal locomotion and the fine motor skills of the hands (Graziano, 2006). The cerebellum has assumed an increasingly important role in motor coordination, but also in action anticipation, a fundamental process for cognitive planning (Stoodley & Schmahmann, 2009).

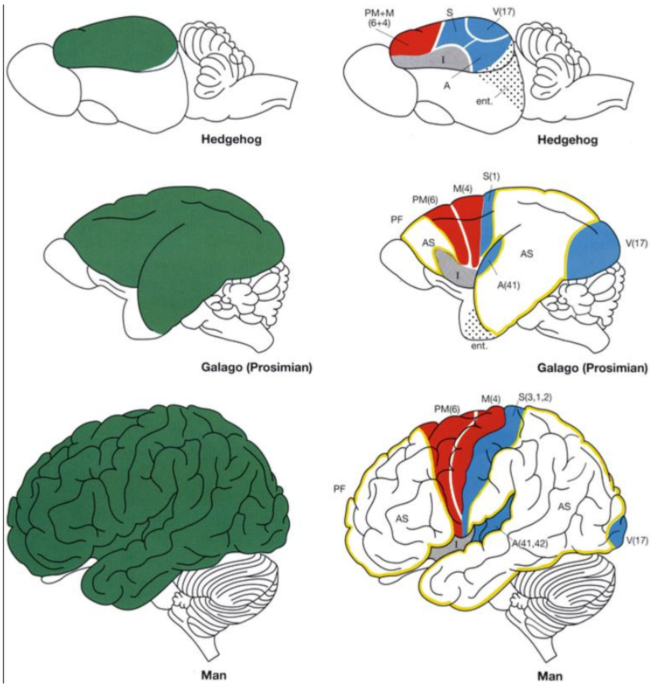


Fig.1: Comparative cortical expansion and motor area specialization across species.
The left column displays total cortical surface, while the right column highlights specific functional areas. In humans, there is a marked enlargement and anterior (rostral) extension of the prefrontal and premotor cortices (red and blue), as well as emergence of specialized regions for somatosensory and auditory processing (blue and yellow). This progressive differentiation, especially in premotor (PM) and prefrontal (PF) areas, underpins the evolution of fine motor control, planning, and tool use associated with bipedalism and hand specialization.

The integration between sensory, motor, and cognitive areas has been strengthened, especially in the parietal and prefrontal areas, which are fundamental for spatial representation, working memory, object manipulation, and the planning of complex sequences (Andersen & Cui, 2009; Fuster, 2008). Complex motor control, manipulation, social interaction, and communication have stimulated the expansion of the prefrontal cortex, the site of executive functions (inhibition, flexibility, planning), working memory, self-regulation, and social understanding (Miller & Cohen, 2001; Diamond, 2013). Finally, walking on two legs involves the management of balance, orientation, and navigation through space. This has favored the development of cognitive spatial maps (posterior parietal area, hippocampus) and prospective thinking, which is crucial for episodic memory and planning (Burgess et al., 2002; Hassabis & Maguire, 2007).

In summary, movement and cognition not only share neural circuits and evolutionary foundations but also influence each other reciprocally. Walking and ego-motion represent a point of convergence between motor activity and complex cognitive processes, through mechanisms of multisensory integration and brain reorganization.

2. Movement complexity

2.1. The concept of movement complexity

Movement complexity can be understood in terms of the number of joints or degrees of freedom (DOF) involved in an action. Bernstein (1967) described this as the “problem of degrees of freedom”: the nervous system must control an enormous variety of possible joint configurations and muscle activations, even in apparently simple tasks. The central question is therefore how the brain reduces or reorganizes this intrinsic complexity to achieve stable, efficient, and adaptable movements.

Early computational models, such as the minimum-jerk approach, framed complexity in terms of trajectory formation. Despite the redundancy of multi-joint actions, executed trajectories tend to be smooth and stereotyped, suggesting that the motor system selects solutions that minimize kinematic costs (Flash & Hogan, 1985). In this sense, redundancy does not produce arbitrary results but is constrained by optimization principles. Optimal feedback control (OFC) further developed this view by treating redundancy as a resource rather than a problem. According to OFC, control policies focus on task-relevant variables and correct deviations only when necessary, following the “minimal intervention” principle (Todorov & Jordan, 2002). Additional joints do not simply add computational load; instead, variability is structured so that surplus DOF are confined to task-irrelevant dimensions. Complexity, in this framework, enables flexibility and robustness. Empirical methods such as the uncontrolled manifold (UCM) approach have provided tools to test these ideas. By partitioning variability into task-relevant and task-irrelevant components, UCM shows that as the number of joints increases, much of the variability is channeled into dimensions that do not compromise performance (Scholz & Schöner, 1999). This indicates that motor control manages complexity by exploiting redundancy rather than suppressing it. The concept of "effective DOF" offers an additional refinement. Although limbs may have many anatomical joints and muscles, biomechanical couplings, tendon constraints, and task geometries reduce the true dimensionality of the control problem (Valero-Cuevas, 2009). Computational methods now estimate this effective dimensionality, showing that apparent increases in complexity are often absorbed by intrinsic mechanical structure (Clewley, Guckenheimer, & Valero-Cuevas, 2008).

At the neural level, muscle synergies have been proposed as another mechanism for simplifying control. Experimental evidence suggests that even highly multi-joint behaviors can be reconstructed from a limited set of synergies, acting as low-dimensional building blocks for complex motor patterns (d'Avella, Saltiel, & Bizzi, 2003; d'Avella & Bizzi, 2005). While the synergy hypothesis remains debated (Tresch & Jarc, 2009), it illustrates the possibility that neural control represents complexity through modular primitives rather than detailed, joint-by-joint specification.

Taken together, these perspectives suggest that movement complexity is not managed through brute-force computation. Instead, it is regulated by multiple complementary strategies: biomechanical constraints that reduce effective dimensionality, optimization principles that channel redundant solutions, control policies that exploit variability, and neural modularity that encodes multi-joint coordination in compact patterns.

2.2. Neural mechanisms involved in motion

The neural control of increasingly complex actions—here defined as the coordination of more joints and neuromuscular elements—relies on the interplay between distributed cortical–subcortical circuits, spinal mechanisms, and biomechanical constraints. At the most peripheral level, the spinal motor pools integrate descending signals with limb biomechanics, transforming muscle activations into joint torques. As the number of joints increases, the combinations of muscle recruitment and coordination multiply, placing greater demands on spinal circuits (Valero-Cuevas, Venkadesan, & Todorov, 2009). Upstream, motor cortical regions adapt population activity to encode higher-dimensional command spaces: M1 represents force- and muscle-related parameters, while premotor and supplementary motor areas (PMd, SMA) contribute to planning, sequencing, and the transformation from abstract goals into joint-specific commands (Grafton, Hazeltine, & Ivry, 1995; Filimon, 2010). Parietal and sensorimotor association areas further mediate coordinate transformations, mapping goal-directed variables in body- and world-centered reference frames, which become increasingly critical as joint complexity grows (Filimon, 2010; Graziano & Aflalo, 2007).

Subcortical structures provide complementary mechanisms for managing complexity. Cerebellar circuits enable precise timing across segments and support rapid error-based corrections, particularly when intersegmental coordination and interaction torques must be predicted (Diedrichsen, Verstynen, Lehman, & Ivry, 2007; Penhune & Doyon, 2002). In parallel, basal ganglia–cortical loops shape action selection, sequence chunking, and the gating of motor programs, becoming especially engaged when tasks involve alternative or hierarchically organized sequences (Grafton et al., 1995; Penhune & Doyon, 2002). Together, these circuits complement cortical planners by modulating initiation, vigor, and structure as task demands rise.

From a computational perspective, complexity is contained through dimensionality reduction. Optimal feedback control posits that the nervous system selects low-dimensional task variables and applies minimal-intervention feedback policies, tolerating variability in task-irrelevant directions while suppressing error in task-relevant subspaces (Todorov & Jordan, 2002). Empirical evidence from the uncontrolled manifold (UCM) method supports this principle: when additional joints are engaged, trial-to-trial variance is preferentially directed into redundant dimensions, while performance-degrading variance is minimized (Scholz & Schöner, 1999).

Dimensionality reduction also emerges from mechanical and neural organization. Biomechanical couplings, tendon constraints, and limb Jacobian structure restrict the effective degrees of freedom, often lowering the true control dimensionality compared to anatomical counts (Valero-Cuevas, 2009). At the neural level, EMG decomposition studies show that multi-joint behaviors can be reconstructed from a small set of time-varying muscle synergies, which act as building blocks for complex patterns across muscles (d'Avella, Saltiel, & Bizzi, 2003; d'Avella & Bizzi, 2005). While the causal role of synergies remains debated (Tresch & Jarc, 2009; Valero-Cuevas et al., 2009), they illustrate how modular primitives may simplify coordination.

Neurophysiological dynamics also scale with task demands. Complex multi-joint actions recruit richer cortical oscillatory patterns, slower predictive activity, and expanded corticocerebellar interactions to anticipate intersegmental torques and sensory consequences (Diedrichsen et al., 2007; Penhune & Doyon, 2002). M1 activity traces higher-dimensional trajectories during planning and execution of multi-joint movements, reflecting the expanded command space (Graziano & Aflalo, 2007; Valero-Cuevas et al., 2009). With practice, however, these demands are reduced: complex action sequences progressively shift from prefrontal and associative reliance toward more efficient cortico-striatal and cerebellar–cortical circuits, supporting smoother and more automated performance (Grafton et al., 1995; Penhune & Doyon, 2002; Guadagnoli & Lee, 2004).

Overall, rising motor complexity increases demands on prediction, coordination, and feedback correction. Yet the nervous system avoids a linear scaling of neural resources by exploiting mechanical constraints, optimization principles, and potential modular primitives. Complexity is thus managed through a distributed strategy: rerouting variance into redundant subspaces, compressing control through biomechanics and synergies, and adaptively shifting reliance among cortical and subcortical circuits as tasks become more demanding (Bernstein, 1967; Flash & Hogan, 1985; Todorov & Jordan, 2002; Scholz & Schöner, 1999; Valero-Cuevas et al., 2009; d'Avella et al., 2003; d'Avella & Bizzi, 2005; Diedrichsen et al., 2007; Grafton et al., 1995; Penhune & Doyon, 2002; Filimon, 2010; Graziano & Aflalo, 2007; Guadagnoli & Lee, 2004).

2.2.1 Reaching

Reaching movements with the arm represent a prototypical model for studying the neural bases of goal-directed motor control, and converging evidence from fMRI, ERP, and single-unit studies has delineated a distributed fronto-parietal–subcortical network supporting their planning and execution. Functional MRI consistently demonstrates the engagement of the posterior parietal cortex (PPC), particularly the superior parietal lobule (SPL) and intraparietal sulcus (IPS), which encode spatial target locations and transform them into limb-centered reference frames for reach planning (Connolly, Andersen, & Goodale, 2003; Filimon, 2010). Within the PPC, the parietal reach region (PRR) exhibits effector-specific selectivity for arm reaching compared to saccades (Connolly et al., 2003; Snyder, Batista, & Andersen, 1997), confirming its central role in visuomotor transformations.

Electrophysiological evidence complements these findings: ERP studies demonstrate early parietal activity (around 200–250 ms post-cue) associated with reach target encoding, followed by later frontocentral components reflecting motor preparation (Praamstra, Kourtis, & Nazarpour, 2009). Source localization analyses indicate that these ERP components originate from PPC and premotor generators, consistent with the temporally staged transformation from sensory to motor representations. The dorsal premotor cortex (PMd) contributes to action selection and trajectory specification, integrating parietal sensory signals with task constraints and translating them into motor plans (Hoshi & Tanji, 2007; Beurze, Toni, Pisella, & Medendorp, 2009). Ventral premotor cortex (PMv) and the anterior intraparietal area (AIP) are additionally recruited when reaching involves object grasping, indicating integration of reach kinematics with hand-shaping synergies (Grafton, Fagg, & Arbib, 1998; Culham, Danckert, DeSouza, Gati, & Menon, 2003). During execution, the primary motor cortex (M1) is robustly engaged, with population codes representing joint torques and muscle activations required for multi-joint coordination (Ehrsson, Fagergren, & Forssberg, 2000). High-resolution fMRI and multivoxel pattern analyses show somatotopically organized and context-dependent activation patterns in M1 during reach and grasp (Schaffelhofer & Scherberger, 2016). Subcortical structures are integral to reach control. The cerebellum is consistently recruited during both visually guided and memory-guided reaching, supporting predictive control and error correction through forward models that anticipate intersegmental dynamics and compensate for sensory delays (Diedrichsen, Verstynen, Lehman, & Ivry, 2007). ERP studies reveal cerebellar contributions to error-related potentials during online correction, particularly in mediofrontal–parietal interactions (MacLean, Watson, & Palmeri, 2017). The basal ganglia, by contrast, contribute to movement initiation, vigor regulation, and sequence selection; fMRI studies show putamen and globus pallidus activation scaling with reach initiation speed and effort (Lehéricy et al., 2006). Connectivity analyses underscore that reaching is supported by dynamic, task-dependent network reconfigurations. fMRI effective connectivity and dynamic causal modeling indicate that cortico-cerebellar and cortico-striatal loops flexibly adjust their weighting depending on accuracy demands and learning stage (Penhune & Doyon, 2002; Steele & Penhune, 2010). These findings align with EEG coherence studies showing transient fronto-parietal synchrony during movement preparation, shifting to stronger fronto-cerebellar coupling during execution (Gross et al., 2005).

Taken together, multimodal evidence converges on a distributed sensorimotor network: posterior parietal areas specify spatial goals and reference frames; premotor regions transform them into action plans; M1 implements execution; and cerebellar and basal ganglia loops optimize timing, accuracy, and selection. ERP data highlight the temporal unfolding of these processes, while fMRI delineates the spatially distributed circuitry. This integration explains how reaching movements achieve flexible, adaptive control in dynamic environments.

2.2.2. Stepping

Reaching movements that require simultaneous stepping represent a paradigmatic case of whole-body coordination, engaging neural circuits that integrate upper limb transport with postural and locomotor mechanisms. Functional neuroimaging has shown that these actions recruit a distributed fronto-parietal–subcortical–brainstem network. Within the posterior parietal cortex (PPC), the superior parietal lobule (SPL) and intraparietal sulcus (IPS) encode spatial goals and transform them into limb-centered reference frames for both arm and leg effectors (Filimon, 2010; Connolly et al., 2003). Recent work by Pitzalis and colleagues has highlighted the dorsomedial parietal area V6A as a critical hub for visuomotor transformations: fMRI and electrophysiological studies indicate that human V6A encodes reach direction, depth, and online corrections, and contributes to the integration of reach planning with locomotor adjustments (Pitzalis et al., 2013; Breveglieri et al., 2023).

Electrophysiological evidence further refines the temporal dynamics of these processes. Event-related potentials (ERPs) and movement-related cortical potentials (MRCPs) demonstrate that parietal activity precedes and drives frontal preparatory processes, with early parietal components (~150–300 ms post-cue) reflecting visuomotor transformations and later frontocentral components reflecting motor preparation. Studies by Di Russo and colleagues have shown that whole-body or multi-effector actions (such as reaching combined with grasping or stepping) are associated with larger preparatory potentials and enhanced parietal source activity, supporting the notion that the PPC specifies spatial goals which are then transformed into motor programs in premotor and supplementary motor areas (Bozzacchi et al., 2012; Di Russo, 2003, 2017).

The premotor cortex (PMC) plays a pivotal role in these transformations, particularly when stepping movements are integrated with goal-directed upper-limb actions. Unlike simple or highly automated locomotor patterns, in which cortical involvement is minimal, the PMC becomes strongly engaged only in complex, non-automatic actions that require precise temporal and spatial coordination between effectors. Within this framework, the dorsal premotor cortex (PMd) integrates parietal inputs and contributes to action selection, trajectory planning, and the coordination of anticipatory postural adjustments necessary for stepping (Hoshi & Tanji, 2007; Beurze et al., 2009). This engagement reflects the PMC's higher-order role in resolving sensorimotor transformations when the motor plan must incorporate both limb transport and balance control. Thus, the activation of the PMC during stepping emerges as a neural marker of task complexity and integrative demand, distinguishing it from the more automatic cortical-subcortical patterns observed during steady walking.

The PMC -and particularly its dorsal division (PMd)- emerges as a key cortical hub for integrating visuospatial information from the parietal cortex with internal motor representations, enabling the generation of predictive and context-dependent motor commands required for complex stepping actions. While simple or automatic locomotor patterns (such as steady-state walking) can be largely sustained by subcortical and brainstem mechanisms with minimal cortical supervision, the PMC becomes strongly and selectively engaged when a motor act requires the integration of upper- and lower-limb effectors, as in reaching while stepping, or when posture must be actively stabilized in the presence of external perturbations (Takakusaki, 2017; Filimon, 2010; Di Russo et al., 2017).

Within this integrative framework, the PMd acts as the cortical interface between visuospatial planning and motor implementation, receiving target-related inputs from the SPL, IPS, and dorsomedial parietal areas (including V6A), and transforming them into dynamic motor trajectories that incorporate both spatial accuracy and postural constraints (Hoshi & Tanji, 2007; Beurze et al., 2009; Pitzalis et al., 2013). This region exhibits preparatory activity well before movement onset, reflecting the encoding of movement vectors and effector coordination plans rather than mere motor execution (Di Russo, 2017; Pitzalis et al., 2019). fMRI and EEG source analyses have shown increased PMd activation during tasks requiring interlimb coupling, anticipatory postural adjustments, or coordination under visual uncertainty, supporting its role in predictive control of complex, whole-body actions (Bozzacchi et al., 2012; Di Russo et al., 2017; Breveglieri et al., 2023).

Notably, Di Russo et al. (2017) demonstrated that during stepping and other complex, multi-effector actions, the PMd exhibits enhanced preparatory activity that temporally follows parietal activation but precedes primary motor recruitment, indicating its hierarchical function in motor program specification and effector coordination. The authors reported a pronounced Bereitschaftspotential (BP) with bilateral PMd generators, reflecting the proactive adjustment of the motor plan to the biomechanical and spatial demands of the forthcoming movement. Complementarily, Pitzalis et al. (2019, 2020) provided fMRI evidence that the dorsomedial visuomotor region V6A maintains reciprocal functional connectivity with PMd during actions requiring combined limb movements and postural control, reinforcing the hypothesis that PMd serves as a convergence site for parietal visuospatial input and motor planning signals. This functional coupling is particularly evident during actions in which hand and foot trajectories must be dynamically co-regulated in external space, as in reaching while stepping or negotiating obstacles (Breveglieri et al., 2023; Pitzalis et al., 2019).

From a functional perspective, the PMC implements a sensorimotor integration mechanism that combines efference copy signals with incoming sensory feedback to predict the kinematic consequences of complex actions. Such predictive coding minimizes sensorimotor delays and allows for adaptive correction of interlimb coordination during the preparatory phase (Shadmehr & Krakauer, 2008; Di Russo et al., 2017). Moreover, intracranial and high-density EEG studies have shown that PMd–SMA synchrony in the beta band increases with task complexity, indexing the cooperative modulation of motor readiness and balance control when stepping is coupled with reaching (Seeber et al., 2014; Bozzacchi et al., 2012).

The supplementary motor area (SMA) and pre-SMA play a critical role in sequencing multi-effector actions, ensuring temporal coupling between reach and step components; fMRI studies of interlimb coordination show increased SMA activation when non-homologous limbs must be synchronized (Debaere et al., 2001). When grasping is combined with reaching, ventral premotor (PMv) and anterior intraparietal (AIP) regions are additionally recruited to integrate hand shaping with the transport and stepping components (Grafton et al., 1998; Culham et al., 2003).

Subcortical circuits are equally critical. The cerebellum supports predictive control and intersegmental coordination, synchronizing arm transport with stepping and adapting to dynamic interaction torques. fMRI and lesion studies show increased cerebellar engagement during tasks requiring multi-limb coordination and rapid error correction (Diedrichsen et al., 2007; Morton & Bastian, 2006). The basal ganglia, particularly the putamen, regulate movement initiation, vigor, and the suppression of competing motor programs when upper- and lower-limb actions are combined (Lehéricy et al., 2006). Brainstem locomotor centers, including the mesencephalic locomotor region (MLR; encompassing the pedunculopontine and cuneiform nuclei), are implicated in step initiation and postural stabilization. fMRI studies of imagined and executed gait demonstrate that these brainstem hubs interact with cortical motor areas and cerebellar circuits during the planning and execution of stepping movements (Jahn et al., 2008; Fling et al., 2013).

Finally, functional connectivity analyses show that cortico-cerebellar and cortico-striatal loops dynamically reconfigure during whole-body reaching. As task complexity increases, coupling between SMA, cerebellum, and parietal regions strengthens, supporting predictive timing and online corrections (Penhune & Doyon, 2002; Steele & Penhune, 2010).

In summary, ERP and fMRI evidence converge to indicate that stepping-related reaching relies on a hierarchical, distributed network: parietal regions (SPL, IPS, V6A) encode spatial goals and visuomotor transformations; the premotor cortex—especially the dorsal division—becomes selectively engaged during complex, integrated actions requiring postural and trajectory coordination; SMA and pre-SMA translate these into temporally coupled multi-effector programs; cerebellum and basal ganglia optimize prediction, timing, and selection; and brainstem locomotor centers ensure postural stability. Together, this network enables flexible and adaptive control of whole-body goal-directed actions, with the PMC acting as a cortical hub that bridges automatic locomotor control and higher-order motor integration.

2.2.3. Walking

Steady-state walking on a flat surface at a constant speed provides an ideal paradigm for investigating the neural mechanisms underlying automatic locomotor control. Converging evidence from neuroimaging and electrophysiology indicates that such locomotion primarily relies on subcortical and brainstem networks, with limited cortical involvement relative to tasks requiring adaptation or obstacle negotiation. Functional MRI and PET studies consistently show robust activation of the supplementary motor area (SMA) and pre-SMA, which are implicated in the initiation, sequencing, and temporal structuring of gait cycles (Hanakawa et al., 1999; Jankowski et al., 2012). The primary motor cortex (M1) exhibits rhythmic activation patterns reflecting ongoing muscle recruitment for step execution, while the primary somatosensory cortex (S1) processes proprioceptive feedback essential for maintaining step symmetry and balance (Christensen et al., 2000; Della-Maggiore et al., 2004). ERP studies complement these findings, showing movement-related cortical potentials (MRCPs) over fronto-central electrodes preceding and during steady-state stepping, with source localization indicating SMA and pre-SMA as principal generators, consistent with their role in movement preparation and initiation (Di Russo et al., 2017; Bozzacchi et al., 2012). Subcortically, the basal ganglia, particularly the putamen, are critical for sustaining automatic locomotor rhythms and regulating step timing and amplitude. fMRI studies demonstrate that basal ganglia BOLD activity correlates with stride frequency and step regularity, supporting their role in automaticity and rhythm maintenance (Jahn et al., 2008; Wu & Hallett, 2005). The cerebellum contributes to predictive control and fine-tuning of interlimb coordination, stabilizing gait and compensating for subtle perturbations (Morton & Bastian, 2006; Diedrichsen et al., 2007). ERP and EEG studies also reveal cerebellar-linked oscillatory activity in the beta and gamma bands during rhythmic stepping, likely reflecting online coordination and sensorimotor integration (Seeber et al., 2014). Brainstem locomotor centers, including the mesencephalic locomotor region (MLR) and the pontomedullary reticular formation, are essential for generating the basic locomotor pattern and ensuring postural stability. fMRI and PET studies show consistent activation of the pedunculopontine nucleus (PPN) and cuneiform nucleus during steady walking, supporting their central role in initiating and maintaining gait cycles (La Fougère et al., 2010; Matsuyama et al., 2004). Functional connectivity analyses indicate dynamic interactions among SMA, basal ganglia, and cerebellum, consistent with parallel cortico-striatal and cortico-cerebellar loops that mediate the automatization of locomotor sequences (Takakusaki, 2017; Iseki et al., 2018). Although steady-state walking is largely mediated by subcortical and brainstem networks, the premotor cortex (PMC)—especially its dorsal subdivision (PMd)—plays a crucial supervisory role in the modulation of locomotor control when gait requires adaptive or context-dependent adjustments. While the SMA and pre-SMA are primarily involved in the initiation and sequencing of gait cycles, the PMC contributes to the integration of visuospatial information and anticipatory postural control, particularly when walking occurs in visually dynamic or unpredictable environments (Hanakawa et al., 1999; Takakusaki, 2017). Neuroimaging and electrophysiological studies indicate that PMd activity increases when locomotion involves goal-directed components—such as obstacle avoidance, target-directed walking, or upper-limb coordination—reflecting its involvement in transforming parietal visuospatial representations into context-specific motor plans (Fling et al., 2013; Filimon, 2010; Di Russo et al., 2017). Evidence from mobile EEG and ERP studies shows that the PMC contributes to early anticipatory components (such as the prefrontal and premotor Bereitschaftspotential, BP) preceding step initiation, indicating its role in predictive motor programming and postural stabilization prior to movement onset (Bozzacchi et al., 2012; Di Russo et al., 2017). This preparatory involvement becomes especially prominent when walking is performed under dual-task conditions or when concurrent upper-limb actions are required, suggesting that the PMC mediates the flexible allocation of neural resources between automatic gait control and higher-order cognitive or motor demands (Al-Yahya et al., 2011; Di Bello et al., 2025). Functional MRI studies further demonstrate that the PMC maintains strong reciprocal connections with parietal visuomotor areas, including the SPL, IPS, and the dorsomedial V6A region identified by Pitzalis et al. (2013, 2019). These connections support a continuous flow of sensory and motor information necessary for the integration of egocentric and allocentric reference frames during visually guided locomotion. In particular, the V6A–PMd pathway appears to be crucial for encoding the spatial trajectory of movement in relation to body orientation and environmental cues, a process fundamental for adaptive gait modulation and dynamic balance (Pitzalis et al., 2019; Breveglieri et al., 2023). Overall, the premotor cortex functions as a cortical interface between automatic subcortical locomotor circuits and higher-order sensorimotor integration networks. While not essential for rhythmic gait generation, its recruitment increases proportionally with task complexity, environmental variability, and the need for visuomotor coordination. In this sense, PMC activity marks the transition from automatic to goal-directed walking, supporting the predictive and integrative aspects of locomotor control that allow humans to navigate dynamically changing contexts (Di Russo et al., 2017; Pitzalis et al., 2019; Takakusaki, 2017).

Taken together, these findings suggest that steady-state walking at constant speed is governed by a hierarchical network: spinal and brainstem central pattern generators produce rhythmic locomotor patterns; cerebellum and basal ganglia optimize timing, coordination, and rhythmicity; and cortical areas, including SMA, pre-SMA, M1, and S1, provide supervisory control and monitoring. ERP and fMRI evidence converge to show that this network allows efficient, stable gait with minimal attentional load, reflecting the neural basis of automatic locomotor control in humans.

3 Dual-Task

Dual-task can be defined as the simultaneous execution of two different tasks, which, by their nature, can be performed independently and separately from one another, characterized by different objectives and distinct parameters that allow for performance measurement (McIsaac et al., 2015). McIsaac et al. (2015) proposed a classification of dual tasks based on two different parameters: novelty and complexity. Novelty concerns the task performer and designates their level of experience; complexity concerns the task itself and can be conceptualized as the degree of interference that the two tasks exert on each other, which is reflected in performance. Based on these parameters, the following are distinguished:

- Easy tasks, characterized by a low level of novelty and a low level of complexity.
- Moderately difficult tasks, in which one of the two characteristics is high and the other low.
- Difficult tasks, where both the level of novelty and that of complexity are high.

Traditionally, the term "interference" refers to a negatively connoted influence, namely a deterioration in performance in one or both tasks, due to the simultaneous execution of a concurrent task. However, at times, a facilitation effect can also be observed, whereby an improvement in performance in one or the other task or in both is seen when they are performed simultaneously.

Plummer et al. (2013) describe nine possible effects on performance resulting from the execution of a Cognitive-Motor Dual Task (DTI):

- no interference, if performance in both tasks remains stable compared to the condition in which the two tasks are performed separately.
- motor interference related to cognitive abilities, if a deterioration is observed only in the motor domain.
- cognitive interference related to motor abilities, if a decline in cognitive performance is observed.
- motor facilitation, if an improvement in performance is observed exclusively in the motor task.
- cognitive facilitation, if an improvement in performance is observed exclusively in the cognitive task.
- cognitive priority trade-off, if an improvement in the cognitive domain and a worsening in the motor domain are observed.
- motor priority trade-off, if an improvement in motor performance and a concomitant decline in cognitive performance are observed;
- mutual interference, if a deterioration in performance in both tasks is observed.
- mutual facilitation, if an improvement in performance in both tasks is observed.

The term “dual-task cost” refers to the percentage of change observed in each of the two individual tasks or in both.

The processes involved in explaining the dual-task cost are primarily attentional. According to Wickens (1980), a competition for attentional resources is at the basis of the observed effects. Pashler et al. (1984) hypothesized the existence of competition between the neural pathways responsible for information processing. Various theories have been proposed to explain the dual-task cost. Each of these explain one or more of the effects described by Plummer et al. (2013). These theories can be classified into four main categories:

1) limited-resource models;
2) interference-based models;
3) facilitation models;
4) dynamic resource-sharing models.

3.1. Limited-Capacity Models

According to limited-capacity models, cognitive resources can be dynamically distributed between different tasks, for example, based on the increased difficulty of one of the two. The latter, therefore, by requiring greater attention, may subtract resources from the other (Kahneman, 1973; Wickens, 1984).

The capacity-sharing theory (e.g., Kahneman, 1973) is based on the assumption that cognitive capacities, in particular working memory, are limited. Consequently, if they must be divided among multiple tasks, they become even more limited (Wickens et al., 1980). In the context of a cognitive-motor dual task (DTI), the two tasks compete for access to such resources, and the cognitive system may not be able to manage them simultaneously in an optimal manner (Pashler, 1984). As a result, performance in each of the two tasks declines (Carrier & Pashler, 1995). However, tasks that are performed automatically do not require access to higher cognitive functions or conscious processing (Schneider & Shiffrin, 1977). Therefore, practice, by automating task execution, makes these resources available again, resulting in improved performance compared to initial trials (Logan, 1988).

The variability and complexity of the environment also play a key role in determining the effects of DTI (Lavie & De Fockert, 2005). In fact, the more complex and changeable an environment is, the greater the amount of cognitive resources allocated to analyzing environmental conditions (Wickens et al., 2008). These resources will be withdrawn from task execution, leading to performance deterioration (Al-Yahya et al., 2011). Conversely, in a predictable and simple environment, most cognitive resources can be directed toward performing the task, allowing for better performance (Beilock et al., 2002).

The multiple-resource theory (Wickens, 1984) maintains that there is not a single attentional resource, a unique central source, but several types of separate resources, such as different sensory channels (e.g., visual, auditory, motor). Two tasks will interfere more with one another the more they draw from the same resource—for example, the same sensory modality. In this case, performance will be limited. However, if the tasks use different resources, it is possible to perform them simultaneously more effectively (Wickens, 2002). Resource allocation, however, is dynamic. As a result, if the difficulty, perceived importance, or urgency of one task increases, cognitive resources may be redirected to it, subtracting them from the other (Wickens & Hollands, 2000). This theory is supported by a study that used a driving simulator to show that tasks sharing the same sensory modality (e.g., visual) interfere more with each other than tasks using different modalities (e.g., visual and auditory) (Horrey & Wickens, 2004).

To test these theories, Wickens et al. (1983) conducted an experiment in which participants were asked to perform different dual tasks composed of combinations of visual or auditory inputs / manual or verbal outputs. The tasks were designed in such a way as to test whether: using the same resources simultaneously (e.g., two visual inputs) would generate more interference; and whether tasks across different modalities (e.g., visual input + verbal output) would cause less interference. The results highlighted that: performance worsened when two tasks shared the same sensory modality or the same response modality, while interference was lower when the modalities differed; the difficulty of one task increased the cost in terms of performance in the other, even without a complete execution block. It follows that not all dual-task interference derives from a serial structural bottleneck. Instead, a dynamic distribution of cognitive resources, which can vary based on the modalities involved and the difficulty of the tasks, explains these observations.

Similar results were found by Tombu and Jolicœur (2003) in an experiment in which participants simultaneously performed two tasks: letter identification (visual task) and sound discrimination (auditory task). The difficulty of each task was manipulated (for example, more similar letters or harder-to-distinguish sounds) to observe how cognitive load influenced reaction times and accuracy. It was observed that performance gradually declined as the difficulty of just one of the two tasks increased, even if the other task remained constant. Moreover, there was never a complete processing block (as predicted by bottleneck theory), but rather a progressive slowdown proportional to the amount of resources absorbed by one task. It can be inferred that cognitive resources are shared, but that there is no fixed point at which processing stops; two tasks can be processed in parallel, but they compete for a limited central capacity. The decline in performance can be explained not by assuming a serial block, but by a suboptimal redistribution of resources.

3.2. Interference-Based Models

Interference theories focus on the emergence of conflict between two tasks that compete for the same cognitive resources.

The bottleneck theory (Malcolm et al., 2015) postulates that when cognitive system overload occurs due to an excessive amount of information to process, a decline in performance in one of the two tasks is observed. This happens particularly when two tasks are processed by the same neural system. Since only one task at a time can be processed, the second task will be processed only after the first one has been completed. Some cognitive processes (e.g., response selection) are more susceptible to this phenomenon than others (Pashler et al., 1994).

Pashler and Johnston (1989) investigated the "bottleneck" in response selection using the PRP (Psychological Refractory Period) paradigm. Participants were asked to perform two simple tasks (e.g., one auditory and one visual) in rapid succession, with a variable interval between the two (SOA – Stimulus Onset Asynchrony). The first task required a vocal or manual response. The second task followed after either a short or a long SOA. This study highlighted that with short SOAs, the reaction time (RT) for the second task increased significantly. However, the reaction time for the first task remained stable, regardless of the interval between the two stimuli. Their results indicate that when two tasks require a response in rapid succession, the response to the second task is delayed until response selection for the first task has been completed, suggesting the existence of a bottleneck in the response selection phase. Furthermore, the bottleneck does not occur during perceptual processing or movement preparation, but specifically during response selection.

However, in a subsequent study exploring the influence of attentional load—by manipulating the complexity of individual tasks and the interval between them—Pashler (1994) observed that performance deteriorates in both tasks when attentional demand is high. This shows that there is not only a rigid bottleneck, but also a flexible and limited sharing of cognitive resources. Therefore, the bottleneck explains the serial aspect of response selection, while capacity-sharing theory explains performance degradation when resources are insufficient.

The Cognitive-Motor Interference Theory (Baddeley & Hitch, 1974; Pashler, 1994; Schmidt & Lee, 2011) suggests that when two tasks draw on the same type of resource, they interfere with one another, leading to reduced performance—unless one of the tasks is automatic or highly familiar, allowing prioritization of the other. Interference increases with the level of task complexity and when the two tasks are similar. Interference may also occur in the case of motor simulation, since imagining or observing an action activates the same areas involved in execution (such as the premotor and motor cortex). Therefore, performing a real motor task while imagining or observing another movement creates neural competition that can degrade performance.

For example, Eaves et al. (2016) proposed a model that describes a spectrum of states combining action observation (AO) and motor imagery (MI), ranging from fully congruent conditions to scenarios in which the contents of AO and MI are in conflict. In these conflict situations, the co-representation of two different actions can be difficult or even impossible to sustain, and representational depth indicators suggest the presence of competition (Eaves et al., 2016).

Al-Yahya et al. (2011) examined prefrontal cortex activation during walking under dual-task conditions in post-stroke patients. Using multimodal imaging techniques, they observed that the simultaneous execution of a cognitive and motor task leads to increased prefrontal activation—an indicator of cognitive overload—and to performance deterioration, highlighting interference between cognitive and motor tasks.

Furthermore, Beilock et al. (2002) conducted a study explicitly aimed at testing whether attention to irrelevant cognitive content selectively interferes with motor tasks, demonstrating a form of specific interference (not just general overload of resources). Participants were asked to perform putts (precision shots) in an indoor mini-golf setting under two experimental conditions. In the first condition (skill-focused attention), the subject had to consciously focus on components of their motor gesture (e.g., wrist position). In the second (divided attention), the subject had to perform a secondary cognitive task (e.g., memorizing letters or solving mental calculations) while putting.

It was found that among novices, the cognitive task did not worsen performance, but excessive attention to movement did; whereas among experts, the cognitive task impaired motor performance, suggesting that interference is specifically linked to competition between automatic motor control and higher cognitive resources. This study demonstrates that cognitive and motor processes can enter into specific competition with one another. Interference does not arise from a mandatory serial processing stage, but rather from a conflict between automatized motor control and simultaneous cognitive processes.

3.3. Facilitation-Based Models

Facilitation models assume that cognitive and motor tasks can interact positively by sharing resources rather than competing for them. This gives rise to a positive interaction between tasks that leads to mutual facilitation (Lauenroth et al., 2016). These models are based on the Functional Synergy Hypothesis, which posits that some tasks, when performed together, can functionally share cognitive and motor resources, creating a synergy between the two activities (Wollesen et al., 2014). This approach contrasts with the traditional view of interference theories, according to which two simultaneous tasks compete for limited resources.

According to this hypothesis, the two tasks can:

- Activate overlapping neural networks, facilitating the transfer of activation from one task to the other (Li & Lindenberger, 2002);
- Have compatible or complementary goals, which allow for joint action planning (Plummer et al., 2013);
- Be automated or well-trained, reducing the load on cognitive supervision (Beurskens & Bock, 2012).

In other words, simultaneous execution can be more effective than separate execution if the neural structures involved cooperate rather than compete.

Moreover, these models predict co-activation, that is, the simultaneous activation of motor and cognitive neural circuits during dual-task execution. This co-activation strengthens the functional connection between motor areas (such as the primary motor cortex, SMA, cerebellum) and cognitive areas (PFC, parietal cortex); it can facilitate neural plasticity, especially in rehabilitative contexts; it improves the central nervous system’s ability to integrate movement with executive, attentional, and decision-making control (Zhang et al., 2024).

From this, the concept of dual-task training (DTT) arises (Silsupadol et al., 2009), a training mode in which a person simultaneously performs two tasks, usually a motor task (e.g., walking, maintaining balance) and a cognitive task (e.g., counting backward, remembering words, making decisions). This modality is used both to improve functional abilities (e.g., in older adults or post-stroke patients) and to test the robustness of motor control under cognitive load.

According to crosstalk theories (e.g., Bayot et al., 2018; Yogev-Seligmann et al., 2008), simultaneous tasks may not interfere with one another if they involve similar sensory inputs and common neuronal populations. In these cases, effective cooperation may occur between the two tasks, leading to performance improvement if one of the tasks plays a facilitating role (Stoykov & Madhavan, 2015). This happens when sensory or motor activities are strongly interconnected or when one task prepares or guides the other. In fact, if the neural system responsible for performing a given task has already been previously activated by another task, access to resources for the second task becomes easier and more immediate (Elsner et al., 2016). This "Cortical Priming" also occurs as a result of mental or visual simulation of a movement that precedes or accompanies another movement (Jeannerod, 2001). Thus, imagery can pre-activate the required neural circuit, facilitating the execution not only of the imagined movement but also of subsequent motor tasks (Gippert et al., 2025), for example by making it faster (Tacchino et al., 2023). This effect is mediated by a more efficient cortical drive to motor units, leading to reduced agonist/antagonist co-activation (Dos Anjos et al., 2022).

For example, Logan & Schulkind (2000) observed that in classification tasks, when both stimuli belonged to the same category (e.g., two letters), facilitation was observed: response times were faster compared to when stimuli belonged to different categories. This effect is attributed to facilitating crosstalk, where the parallel activation of compatible responses between the two tasks reduces interference and improves overall performance.

Koch (2009), on the other hand, conducted an experiment in which participants simultaneously performed a visual task (object identification) and an auditory-manual task (response to sounds). When the responses required by the two tasks were spatially compatible (e.g., both on the left or both on the right), a reduction in dual-task costs was observed compared to conditions with incompatible responses. This suggests that the overlap of response codes can facilitate the simultaneous execution of two tasks, supporting the idea that crosstalk can have positive effects when responses are congruent.

The motor and cognitive facilitation theory (Schmidt & Lee, 2011; Lee & Schweighofer, 2009) suggests that cognitive and motor tasks can be performed simultaneously, generating performance facilitation, especially when motor movements become automatic or when tasks are performed with low cognitive difficulty. This is because performing an easy or automatic task frees up resources that can be employed to carry out another, more complex task (Lee & Schweighofer, 2009). In fact, this theory is based on the assumption that motor task execution also draws on cognitive resources due to the strong interconnection between the motor and cognitive systems. Consequently, automating the motor task frees up cognitive resources. Moreover, due to this interconnection, training in both the motor and cognitive tasks simultaneously leads to mutual reinforcement through the formation of neural circuits that encode the combination of the two (Surkar et al., 2025). This perspective is well explained by the mechanisms described in the concept of cortical priming, i.e., the pre-activation of neural networks responsible for a specific task through prior stimulations, such as motor imagery or the execution of related tasks (Jeannerod, 1994; Pascual-Leone et al., 1995). When, for example, a motor task is imagined or prepared before executing another task (even a different one), it can trigger pre-activation of the motor cortex, thus facilitating subsequent execution and reducing dual-task costs (Gippert et al., 2025; Dos Anjos et al., 2022). Therefore, it can be hypothesized that the facilitation between cognitive and motor tasks observed by Schmidt and Lee is partly mediated by a cortical priming effect, in which neural pre-activation facilitates shared resource management between the two tasks, improving the efficiency of the integrated cognitive-motor system.

These theories are supported by the study of Mirelman et al. (2014), which evaluated the motor performance of older adults walking alone and walking while performing a simple cognitive task, such as naming or forward counting. In some subjects, the presence of the cognitive task improved step regularity and stability compared to walking alone. This positive effect was attributed to increased attention and executive regulation, which favor better postural control.

Salvucci & Taatgen (2011) specifically demonstrated how cognitive and motor skills can be combined and integrated over time through practice, since a “structural integration” would allow the brain to optimize the simultaneous management of two tasks with shared components. In this case, participants performed a primary task (real driving) and a secondary task (e.g., responding to messages). With repeated simultaneous training, rather than with practice of the individual task alone, participants developed automated strategies that allowed efficient and safe management of the tasks, even in complex conditions. The integration of the two activities was made possible through shared neural patterns and anticipatory response planning.

The skill integration theory (Schmidt & Lee, 2011) asserts that acquiring new skills that enable the simultaneous and integrated performance of two tasks, or repeated practice of a task combination, allows for the automation of both tasks. Therefore, learning and practice free up cognitive resources that can be reinvested to further improve performance, rather than merely maintain it. Moreover, unlike crosstalk theory, this model does not concern the facilitative effect that one task may have on another, but rather the ability to perform a specific combination of tasks simultaneously in a synergistic and integrated way.

Koch et al. (2018) tested this theory in a study in which participants were asked to repeatedly perform a visual task (e.g., letter classification) and an auditory task (e.g., sound classification) together or separately. The results showed that simultaneous learning and practice improved efficiency in joint task management, as well as reaction times and accuracy in individual tasks, and also led to greater automation of the interaction between the two tasks. This was due to the development of co-representations, i.e., integrated representations of the two tasks, which significantly reduced the dual-task cost.

3.4. Dynamic Resource-Sharing Models

Dynamic resource-sharing models (Norman & Shallice, 1986) explore the capacity to dynamically distribute cognitive resources across tasks based on their difficulty and priority. These models were developed in contrast to more rigid theories and may be considered an evolution of them. They describe cognitive processes as dynamic and flexible, and the cognitive system as capable of adapting in real time to changes in task difficulty and cognitive load, individual intentions, and contextual environmental factors, by redistributing resources accordingly. These models represent the most modern and integrated approach to explaining variability in dual-task outcomes.

These models are based on the concept of co-activation, as during dual-task training, the organism learns to efficiently redistribute resources between cognitive and motor domains; the progressive automation of one of the two tasks (typically the motor task) frees up resources for the other; and attentional flexibility develops, enabling better overall performance.

The adaptive model of executive control and resource allocation (Norman & Shallice, 1986; Burgess et al., 2007; Meyer & Kieras, 1997) proposes that the simultaneous execution of tasks depends on adaptive executive control mechanisms that decide, in real time:

- whether tasks should be performed in parallel or in sequence (explaining cases of serial processing),
- whether to allocate attentional resources selectively (explaining cases of interference),
- whether, in the presence of well-established automatisms, tasks can be executed with mutual facilitation.

In the experiment by Meyer & Kieras (1997), participants performed two tasks in rapid succession, with variable time intervals between the presentation of the first stimulus (T1) and the second (T2). When T2 was presented immediately after T1, the response to T2 was significantly delayed, indicating interference due to the serial processing necessary to avoid cognitive overlap. However, as the interval between the two tasks increased, the delay in T2 response decreased, suggesting that the cognitive system can adapt and allow more parallel processing when conditions permit. These results highlight that executive control dynamically regulates the mode of execution (parallel or serial) and the allocation of attentional resources, based on the difficulty and priority of the tasks, thus supporting the adaptive model of executive control and resource allocation.

Supporting the adaptive executive control model and dynamic resource-sharing, Al-Yahya et al. (2011) conducted a systematic review of 66 experimental studies investigating the effects of cognitive-motor dual-tasking. The cognitive tasks examined varied in type (memory, attention, inhibition, decision-making), complexity, and mental load, while the motor component primarily involved walking in free or structured conditions (e.g., on a treadmill). The review found that the presence of a second cognitive task negatively influences motor performance (e.g., reduced gait speed, increased variability and instability) and, conversely, that motor demands can impair cognitive response accuracy or speed.

However, this effect is modulated by several factors that influence attentional resource allocation. In particular, the difficulty of the cognitive task modulates the amount of resources required: more complex tasks (e.g., n-back or rapid decision-making tasks) demand greater attention and cause more deterioration in walking. Similarly, the level of motor task automatization plays a key role: in younger or more practiced individuals, walking requires less conscious control, allowing for better management of cognitive load. An additional modulation occurs through priority instructions: when participants are instructed to prioritize one of the two tasks, the cognitive system redistributes resources accordingly, improving the performance of the prioritized task at the expense of the other. Finally, repeated practice in dual-tasking contributes to automating one or both tasks, reducing competition for resources and promoting smoother processing.

The Dynamic Interference and Context Model (Wickens, 2002; Tombu & Jolicoeur, 2003; Fischer & Plessow, 2015) assumes that interference or facilitation does not depend on a single theory, but on:

- The type of task (sensory, cognitive, motor),
- The level of automatization,
- The overlap in cognitive resources,
- Contextual constraints (environment, priority, workload).

Cognitive flexibility allows for selecting between parallel or serial processing modes depending on context, difficulty, and task relevance.

For example, Fischer & Plessow (2015) showed that the cognitive system manages multitasking by flexibly choosing between parallel and serial processing depending on factors such as task difficulty, priority, and context. To investigate this, participants were asked to perform two tasks simultaneously: a simple visual discrimination task (e.g., quickly identifying the shape or color of a visual stimulus such as a circle or square) and a second discrimination task, which could be visual or auditory and whose difficulty was experimentally manipulated by increasing stimulus ambiguity or reducing exposure time. Both tasks required distinct manual responses. The results showed that when the second task was easy or less prioritized, participants were able to process both tasks in parallel with little interference; however, when the second task became more difficult or more important, a clear tendency toward serial processing emerged—that is, completing one task before starting the other to reduce errors and cognitive overload. This experiment demonstrates the brain’s capacity to dynamically adapt its processing strategy based on immediate demands, supporting a model of dynamic and flexible cognitive interference that goes beyond rigid models of exclusively serial or parallel processing.

The study by Leone et al. (2017) also examined the cognitive mechanisms underlying cognitive-motor dual-tasking, investigating how the simultaneous execution of a motor task (walking on a treadmill) and a visual discrimination task is influenced by key variables such as cognitive difficulty, assigned task priority, and practice level. Participants were asked to recognize target visual stimuli (e.g., shapes or colors) presented on a screen while walking, and experimental conditions varied by stimulus complexity, priority instructions (focus on walking vs. focus on the cognitive task), and number of trials (to assess repetition effects).

The results showed that, as the cognitive task became more difficult, marked interference occurred in motor performance: walking speed decreased, gait variability increased, and gait stability was reduced. When priority was given to maintaining gait, motor performance improved, but at the cost of reduced accuracy and response speed in the visual task. Furthermore, with training, both tasks were managed more efficiently: mutual interference decreased, suggesting that practice promotes automatization of the motor task and allows for more flexible and strategic management of cognitive resources.

MODEL	Limited-Capacity Models	Interference Models	Facilitation Models	Dynamic Resource-Sharing Models
ASSUMPTION	Cognitive resources are fixed, centrally controlled, and available in limited quantity	Cognitive or sensory resources are in conflict between the two tasks	Tasks share resources synergistically or automatically	Resources are flexible and adaptive
OBJECTIVE	To analyze structural or functional limitations of resources	To explain the interference effect	To explain the facilitation effect	To study how resources are flexibly distributed
RESOURCE DESCRIPTION	Single	Shared or overlapping (e.g., sensory channels)	Arising from the use of the same underlying processes or activation of the same networks	Contextual (Multiple and dynamic (e.g., motor, cognitive, sensory…)
PHENOMENOLOGICAL EXPLANATION	System overload	Conflict in accessing the same resource, mutual interference between tasks	Automatization, compatibility of underlying processes, neural network sharing	Contextual (based on goals, difficulty, urgency, training, etc.)
EXPERIMENTAL EVIDENCE	Systematic delay in the second task as SOA decreases	Reduction in performance in terms of RT or accuracy	Improvement in dual-task performance over single-task	Improvement through practice, reduced interference, strategic flexibility
TYPE OF INTERACTION EXPLAINED	Limitation	Negative interference	Facilitation	Interference, facilitation, or neutrality

APPLICATION DOMAIN	Sequential tasks, neuropsychological studies	Ergonomics, stress-based driving	Rehabilitation, dual-task training, performance optimization	Training, multitasking, rehabilitative and athletic contexts

Tab. 1. : Comparison of four theoretical models of cognitive resource management in dual-task situations.

In conclusion, the strategy the brain adopts during dual-tasking depends on a complex interaction between environmental factors, specific characteristics of the tasks, and the instructions or priorities given to the performer. Environmental factors, such as the complexity and predictability of the environment, modulate the amount of cognitive resources available: in complex or changing environments, more resources are engaged in external monitoring, increasing the likelihood of interference and of relying on the bottleneck model, where tasks are processed sequentially to avoid overload.

Task characteristics—such as difficulty, novelty, similarity between tasks, and level of automatization—determine whether the required resources overlap, promoting interference, or whether the tasks can instead facilitate each other through automatization or the use of common neural circuits, as described in facilitation and crosstalk models.

Finally, instructions and assigned priorities directly influence the distribution of attentional resources, pushing the cognitive system to choose a parallel or serial mode of execution, as predicted by dynamic resource-sharing models and adaptive executive control. For example, if a task is considered more urgent or prioritized, the brain may allocate more resources to it, slowing down or suspending the processing of the other task in order to minimize errors.

This capacity to dynamically modulate multitasking strategies allows for efficient and flexible adaptation to contextual demands, optimizing overall performance in dual-task situations.

3.5. ERP and CMDT

The simultaneous execution of a motor task, such as walking, and a secondary cognitive task (e.g., selective attention, working memory, or decision-making) is often used to investigate attentional–motor interactions. This approach is particularly relevant in dynamic and unpredictable environments. In this context, ERPs provide neural indices that reflect cognitive load, attentional allocation, and variations in stimulus–response processing efficiency (Makeig et al., 2009).

One of the most studied ERP components in dual tasks is the P3. Numerous studies have shown that, during walking, P3 amplitude significantly decreases compared to the condition in which the cognitive task is performed while standing or sitting, indicating interference between the two domains due to competition for limited cognitive resources (De Sanctis et al., 2014; Gramann et al., 2011).

This effect is particularly evident in older adults or individuals with cognitive decline, suggesting that walking, although automated, requires higher cognitive resources under neurological vulnerability or during complex cognitive tasks (Beurskens & Bock, 2012; Mirelman et al., 2014). ERPs have also proven sensitive to variations in motor task complexity: the amplitude of the P300 tends to decrease further when walking is performed on uneven terrain or with obstacles, reflecting an increased attentional load to maintain postural stability (Debener et al., 2012).

In addition to the P3, other ERP components have also proven useful for studying locomotion under dual-task conditions. The N2 and N1 components, associated respectively with stimulus-response conflict and early sensory stimulus processing, show amplitude reduction and latency increase during walking, indicating a slowing of automatic cognitive processes induced by motor engagement (Ladouce et al., 2019; Malcolm et al., 2015).

The integration of electroencephalography with mobile technologies (Mobile Brain/Body Imaging – MoBI) has revolutionized the study of ERPs in dynamic contexts, allowing for brain activity recording during real-world locomotion (Gwin et al., 2010; Gramann et al., 2014). This approach overcomes the limitations of static laboratory paradigms, offering a more realistic view of the neural processes involved in complex motor behavior. For example, Gwin et al. (2010) used high-density EEG combined with motion capture to analyze brain activity fluctuations during treadmill walking, highlighting P300 suppression under cognitive dual-task conditions.

3.6. CMDT in sport

In the sports domain, the CMDT paradigm has been widely used to investigate the interaction between cognitive processes and motor control, highlighting how the simultaneous management of multiple tasks is crucial for performance in real game situations, often characterized by complex information processing under pressure. In many sports, athletes must make rapid decisions while performing complex motor actions. The dual-task approach allows for the analysis of how divided attention, working memory, and executive functions influence motor efficiency and, conversely, how motor load can interfere with cognitive performance.

Numerous studies have shown that performing a cognitive task simultaneously with a sports action (e.g., dribbling, running, jumping) can impair or alter performance quality, especially in less experienced athletes (Beilock et al., 2002). This phenomenon is particularly evident in beginners who, not yet having automated motor patterns, require greater attentional resources for motor task execution (Beilock et al., 2002). In these individuals, the addition of a cognitive task leads to significant deterioration in both motor and cognitive components, suggesting mutual interference due to competition for limited attentional resources (Kahneman, 1973). In contrast, expert athletes appear able to automate many motor components, freeing up cognitive resources for secondary task management (Woollacott & Shumway-Cook, 2002).

The secondary tasks used in dual-task protocols can be cognitive (e.g., solving arithmetic operations, responding to verbal stimuli), perceptual (e.g., identifying visual or auditory signals), or decisional (e.g., choosing which teammate to pass the ball to). Studies conducted on athletes under dual-task conditions have shown that working memory overload is associated with reduced motor precision, especially in dynamic contexts (Leone et al., 2017). In expert individuals, the automatization of motor routines allows working memory to be disengaged, making it available for tactical or strategic processing. In such individuals, many components of motor action are executed automatically, with less dependence on executive functions for movement control, thus increasing cognitive efficiency: while basic gestures are performed effortlessly, cognitive resources can be devoted to managing complex or unexpected tasks (Woollacott & Shumway-Cook, 2002). A clear example is that of a professional tennis player, able to respond to a fast serve while simultaneously anticipating the opponent's position and planning the next move.

In less experienced individuals, interference between motor and cognitive tasks is generally more marked, as movement execution still requires a high degree of voluntary control, limiting the availability of resources for cognitive processing (Furley & Memmert, 2010). In such cases, motor activity in dual-task context may be less fluid, more imprecise, and prone to error. A study on youth soccer players showed that during a dribbling task combined with a tactical decision, inexperienced players exhibited slower reaction times and a significant reduction in precision compared to their more experienced peers (Vestberg et al., 2012).

The nature and difficulty of the secondary task significantly influence the degree of observed interference (Pashler, 1994). A high cognitive load increases the risk of motor errors or reaction time delays (Abernethy, Maxwell, Masters, Van Der Kamp, & Jackson, 2007). Furthermore, under physical or mental fatigue, dual-task performance tends to further deteriorate, highlighting the vulnerability of executive functions and attentional capacities under stress (Smith, Marcora, & Coutts, 2015). This is particularly relevant in endurance sports or in high-pressure moments, such as the final minutes of a match.

3.6.1 Dual task training

In recent years, dual-task training has emerged as a highly effective strategy for enhancing sports performance, especially in dynamic and unpredictable disciplines such as soccer, basketball, and tennis. These sports require continuous adaptation to changing stimuli and simultaneous processing of multiple pieces of information, where athletes must make quick decisions while performing complex motor actions. In this context, the integration of cognitive and motor training represents an innovative approach to developing fundamental skills such as selective and divided attention, cognitive flexibility, and motor adaptability (Faubert & Sidebottom, 2012; Diamond, 2013).

The principle of dual-task training involves inserting a second cognitive task (e.g., solving simple arithmetic operations, responding to verbal stimuli, memorizing sequences, or real-time decision-making) during the execution of a motor task (e.g., running, dribbling, passing). This method stimulates the athlete’s ability to manage cognitive load while maintaining the quality of motor performance, increasing the efficiency of the mind-body system (Leone et al., 2017).

Numerous scientific studies confirm the benefits of this methodology, especially in youth sports. For example, the study by Vestberg et al. (2012) showed that young soccer players undergoing training with integrated cognitive tasks (such as problem-solving during technical drills) demonstrated significant improvements in executive functions and decision-making capacity, with positive impacts on on-field performance. These athletes, compared to a control group, were quicker in interpreting the game and more effective in tactical decisions under pressure.

Faubert and Sidebottom (2012) also demonstrated through a perceptual-cognitive training paradigm in immersive environments that systematic exposure to dual tasks improves selective attention and short-term visual memory, which are fundamental elements in high-paced sports. Elite athletes in sports such as hockey and American football showed a greater capacity for simultaneous information processing than untrained individuals, suggesting the potential transferability of these benefits to actual performance.

More recently, controlled trials with Cognitive-Motor Dual-Task (CMDT) training have provided converging evidence of its efficacy in both sports and clinical populations. Studies on youth and semi-professional athletes showed that CMDT protocols not only enhanced technical-tactical skills but also improved executive functions such as working memory, divided attention, and cognitive flexibility (Lucia et al., 2021; Casella et al., 2022). These behavioral improvements were paralleled by neurophysiological changes, with increased efficiency in anticipatory ERP markers of sensory and motor preparation (e.g., pN, Bp, vN) and post-stimulus components related to decision-making and attentional allocation (e.g., P3), confirming the neural plasticity induced by dual-task training (Di Russo et al., 2019; Lucia et al., 2023).

Another area of investigation has highlighted the potential of dual-task training in injury prevention. Some studies on adolescent athletes have shown that inserting cognitive tasks during dynamic movements promotes improvements in neuromuscular control and postural stability, reducing the risk of motor errors under cognitive load (Grooms, Page, & Onate, 2015; Sidelnik & Hootman, 2020).

It has also been shown that dual-task training has positive effects on mental resilience and the ability to maintain high performance under fatigue. Practice in cognitively demanding contexts increases tolerance to interference and improves management of competitive stress (Furley & Wood, 2016), which is particularly useful in sports requiring mental clarity in critical moments.

The literature further suggests that the effects of dual-task training are modulated by the level of expertise. Beginners tend to experience greater interference between tasks, while expert athletes, thanks to the automatization of motor skills, can sustain higher cognitive loads during performance (Beilock et al., 2002; Woollacott & Shumway-Cook, 2002). This highlights the need for a progressive approach to introducing dual-task: initially with simple and separate tasks, then gradually increasing their complexity and interactivity.

From an applied perspective, this framework implies practical and evidence-based: assessing athletes under dual-task conditions to identify vulnerabilities that emerge only under cognitive load (systematic evidence); gradually integrating CMDT elements into training programs (from simple to complex tasks, modulating sensory and decisional demands) so that motor automatization allows for cognitive transfer; using ERPs and neurophysiological measures (BP, pN, vN, P3) as objective markers of training-induced plasticity and of the ability to reallocate resources in game situations (Lucia et al., 2021; Casella et al., 2022; Wu et al., 2024).

Finally, the integration of basic research with applied studies in athletes suggests that improving anticipatory preparation (sensory and motor readiness) and multisensory integration capacity is key to transferring neurocognitive gains to on-field performance, reducing interference in situations of high cognitive-motor demand.

3.6.2. The diagnostic use of CMDT in sport

The dual-task paradigm is also used as a diagnostic tool to identify cognitive deficits in injured athletes, for example following a concussion. A reduced ability to manage dual tasks can indicate incomplete recovery of cognitive functions (Howell, Osternig, Chou, & King, 2014). In addition to its application in performance, the paradigm has proven to be a valid clinical and rehabilitative tool for identifying residual cognitive deficits after head trauma. In such cases, assessing the athlete's ability to perform cognitive and motor tasks simultaneously provides a sensitive measure of the functional state of the central nervous system.

Numerous studies have shown that, despite apparent motor recovery, athletes with recent head trauma show persistent difficulties in managing simultaneous tasks (Howell, Osternig, Chou, & King, 2014). In particular, their performance is significantly worse in dual-task compared to healthy individuals or to their pre-injury condition, indicating that executive functions, working memory, and divided attention may not be fully restored even in the absence of subjective symptoms.

The dual-task test is therefore a more sensitive and ecologically valid tool than traditional neuropsychological tests, as it simulates cognitive stress conditions comparable to those in sports practice. Howell et al. (2014), for example, showed that concussed athletes exhibit altered postural stability and reactivity when performing a motor task (e.g., walking, jumping) combined with a cognitive task (e.g., backward counting, responding to verbal stimuli). These dual-task deficits are often present even after a return to apparently normal clinical status, suggesting that cognitive recovery may take longer than symptom resolution.

Other studies have shown that post-concussion dual-task deficits primarily involve frontoparietal networks, implicated in attentional control, planning, and cognitive load management (Parker et al., 2005; Catena, van Donkelaar, & Chou, 2007). These alterations are associated with an increased risk of recurrence and a higher likelihood of motor errors during return to sport, underscoring the importance of including cognitive assessments in Return to Play (RTP) protocols.

The integration of the dual-task paradigm in RTP protocols is thus increasingly widespread, aiming not only to verify post-injury functional integrity but also to prevent premature returns and reduce the risk of new injuries. Some authors propose the use of complex, difficulty-modulated dual tasks as an integral part of cognitive-motor rehabilitation (Broglio et al., 2015; Fino, Parrington, & Muthalib, 2016), to progressively make athletes more resilient to the cognitive and decisional stress typical of the competitive environment.

In conclusion, the use of the dual-task paradigm in sports and clinical settings allows for a more accurate assessment of the recovery of higher cognitive functions, representing a key element in modern evaluation and prevention protocols, ensuring safety and effectiveness in returning to competitive activity.

3.7. Movement complexity in cognitive-motor dual-task

Increasing motor complexity—operationalized in terms of the number of joints involved, intersegmental coordination requirements, and variability of the response—systematically impacts both behavioral performance and underlying neural mechanisms. Classic behavioral studies demonstrated that more complex responses are associated with longer reaction times and decreased accuracy (Henry & Rogers, 1960; Christina, 1982; Anson, 1982), and more recent work has linked these changes to specific cortical and subcortical dynamics. Simple, highly automated motor acts, such as pressing a single key or steady walking on a flat surface, rely primarily on subcortical and spinal circuits (e.g., central pattern generators, mesencephalic locomotor region), imposing minimal cognitive load and showing negligible impact on concurrent cognitive task performance (Jahn et al., 2008; Al-Yahya et al., 2011). By contrast, as motor responses become more complex—such as multi-joint postural adjustments, obstacle negotiation, or combined limb actions—reaction times increase, accuracy declines, and cortical recruitment expands, engaging higher-order circuits including the dorsolateral prefrontal cortex (DLPFC) and anterior cingulate cortex (ACC) to mediate attentional allocation, monitoring, and task switching (Yogev-Seligmann, Hausdorff, & Giladi, 2008; Al-Yahya et al., 2011; McPhee & Mears, 2022).

Electrophysiological markers provide converging evidence: the Lateralized Readiness Potential (LRP), a robust index of motor preparation, scales in amplitude and latency with response complexity, reflecting the increased duration and intensity of motor program instantiation in multi-joint responses (Hackley et al., 1995; Smulders & Miller, 2012; Schmitz et al., 2019). Early components such as the N2 are enhanced when response selection and inhibition demands rise, while the P3 shows latency shifts and amplitude modulation as attentional resources are redistributed toward managing complex motor programs (Patel & Azzam, 2005; Folstein & Van Petten, 2008; Enriquez-Geppert et al., 2010). At the same time, EEG and Mobile Brain/Body Imaging (MoBI) studies demonstrate increases in frontal midline theta and parietal alpha during complex dual-task conditions, predicting decrements in cognitive accuracy and longer reaction times when motor demands surpass the capacity of automatic control systems (Gramann et al., 2011; Makeig et al., 2009).

Functional neuroimaging supports these electrophysiological findings: fMRI studies show that the supplementary motor area (SMA) and dorsal premotor cortex (PMd) increase their activation with motor sequence length and intersegmental coordination demands, enabling anticipatory postural adjustments and precise multi-joint timing (Diedrichsen & Kornysheva, 2015;

Halsband & Lange, 2006). The posterior parietal cortex (PPC), including superior parietal lobule and intraparietal sulcus, is recruited to transform spatial goals into joint-specific motor commands, while maintaining execution stability under high complexity (Filimon, 2010). Subcortical circuits also play critical roles: the basal ganglia support sequence chunking and automatization, thereby reducing cognitive load during well-learned complex movements, while the cerebellum predicts and corrects intersegmental errors, a function that becomes increasingly vital as motor variability grows (Grafton et al., 1995; Imamizu et al., 2000; Morton & Bastian, 2006). These processes are complemented by stronger functional connectivity between frontoparietal executive networks and sensorimotor–cerebellar circuits during high-complexity tasks, reflecting the redistribution of limited attentional resources across motor and cognitive domains (Wu et al., 2013; Mehta et al., 2012; Wilkins et al., 2020; Chung et al., 2023).

Behaviorally, this interplay manifests as systematic dual-task costs: increasing motor complexity slows reaction times, reduces working memory accuracy, and often elicits a prioritization of motor stability over cognitive performance—the so-called “posture-first” strategy (Al-Yahya et al., 2011; McPhee & Mears, 2022; Boisgontier et al., 2014; Bhagat et al., 2024). Recent findings further suggest that parts of motor programming can overlap with execution in complex movements, which may reduce reaction times in certain contexts, but only at the expense of greater reliance on SMA, cerebellar, and prefrontal monitoring mechanisms (de Xivry et al., 2016; Mawase et al., 2018).

In summary, rising motor complexity shifts the neural substrate from predominantly subcortical and spinal mechanisms toward distributed cortical–subcortical networks—including SMA, PMd, PPC, DLPFC, ACC, cerebellum, and basal ganglia—resulting in graded behavioral costs in both motor and cognitive performance. ERP components (LRP, N2, P3), oscillatory markers (theta, alpha), and fMRI activations converge to show that as the number of joints and coordination demands increase, dual-task interference becomes stronger, reflecting a systematic interaction between the dimensionality of motor control and the allocation of cognitive resources (Henry & Rogers, 1960; Yogev-Seligmann et al., 2008; Al-Yahya et al., 2011; Gramann et al., 2011; McPhee & Mears, 2022)

4 Neural Basis of self-motion perception

4.1. Egomotion and Multisensory Integration: Neural Foundations and Cognitive Implications

Walking—and more generally, egomotion, meaning the movement of one’s own body through space—constitutes a complex motor activity that involves the continuous updating of bodily and environmental representations. This activity requires the integration of signals from multiple sensory systems, in a process known as multisensory integration (MI).

As highlighted by Greenlee et al. (2016) in a systematic review, the experience of bodily movement through space results from the convergence of proprioceptive, visual, vestibular, and, to a lesser extent, auditory information. These inputs must be coherently processed to ensure postural balance, spatial orientation, trajectory regulation, and the ability to interact effectively with the surrounding environment. The accuracy and efficiency of locomotion thus depend on the brain's ability to simultaneously fuse heterogeneous, and often noisy or ambiguous, sensory inputs into a unified and stable representation.

At the neural level, the circuits responsible for multisensory integration involve a distributed network that includes:

- The cerebellum, which integrates proprioceptive and vestibular signals to modulate balance and motor anticipation (Massion, 1992; Miall & King, 2008);
- The insula, crucial for bodily awareness and interoceptive processing, as well as for sensorimotor integration (Craig, 2009);
- The posterior parietal cortex, involved in space-for-action representations, sensorimotor transformations, and spatial attention (Andersen & Cui, 2009; Buneo & Andersen, 2006);
- The medial superior temporal area (MST), specialized in encoding optic flow and detecting motion in the visual space (Duffy, 1998);
- The premotor area, which contains multisensory neurons and participates in programming actions directed at multisensory stimuli (Graziano & Cooke, 2006).

These areas interact dynamically, modulating not only spatial navigation and motor control, but also higher cognitive functions such as selective attention, time perception, the construction of bodily self-awareness, and agency (Tsakiris et al., 2007; Blanke, 2012). In particular, multisensory integration is closely tied to the formation of the sense of self in bodily and social space, contributing to body image and to the distinction between “self” and “other.” The importance of egomotion for cognitive development is especially evident in childhood.

According to Thelen & Smith (1994), the acquisition of autonomous walking is not merely a motor milestone but represents a crucial cognitive transition. Spontaneous movement through the environment stimulates the development of both egocentric and allocentric spatial representations, strengthens proprioception, and contributes to the construction of body image. The ability to actively explore surrounding space changes the perception of the environment and enhances the ability to predict the effects of one's actions—fundamental for building intentionality and causal reasoning.

In this sense, the experience of movement through space (particularly self-initiated walking, which involves the active generation of egomotion) is key not only for the maturation of sensorimotor networks, but also for the development of higher cognitive functions such as spatial memory, planning, and even language, through interaction between the motor system and higher associative areas (Iverson, 2010).

In adulthood, the multisensory integration related to locomotion remains a dynamic and adaptive process, essential for maintaining balance and for navigating complex environments. Recent studies have shown that alterations in multisensory integration (e.g., via manipulation of optic flow or under virtual reality conditions) can modify movement perception, slow reaction times, alter posture, or induce sensorimotor conflicts—with important clinical and rehabilitative implications (Campos et al., 2012).

The link between movement and cognition is not unidirectional, but these processes influence each other reciprocally and mutually. Movement, in fact, is not the mere product of automatic motor mechanisms, but represents the outcome of a complex and dynamic cognitive elaboration. Cognitive processes influence movement at various levels, from planning to execution, involving a wide network of cortical and subcortical structures. First of all, selective attention is fundamental to direct action towards relevant goals and to adapt motor behavior to environmental demands. In dynamic or unpredictable environments, attention allows distracting stimuli to be filtered, focusing cognitive resources on the motor target (Posner & Petersen, 1990; Corbetta & Shulman, 2002). Attentional selection also guides the motor system in managing interference and prioritizing action, for example during dual tasks or in crowded environments. Another crucial aspect is the role of working memory in motor planning. This cognitive component temporarily maintains relevant information for the realization of an action sequence, allowing the subject to update and monitor their movements in real time (Baddeley, 2003; Fuster, 2008). Interactions between the dorsolateral prefrontal cortex, premotor and parietal areas are essential for building flexible and adaptive motor representations. Executive functions regulate the initiation, inhibition, adaptation, and monitoring of actions. In particular, inhibitory capacity is fundamental to suppress inappropriate or premature motor responses, as demonstrated in Go/No-Go or Stop-Signal tasks (Aron et al., 2004; Miyake et al., 2000). These functions are based on a network that includes the prefrontal cortex, anterior cingulate cortex, and basal ganglia, structures implicated in decision-making processes. An additional cognitive contribution to motor skills derives from prediction and anticipation of movement, abilities supported by the cerebellum and posterior parietal cortex. These structures build internal models that allow the nervous system to predict the sensory consequences of a movement before it is executed, making the action smooth and correct even under uncertain conditions (Wolpert, Ghahramani, & Jordan, 1995; Shadmehr & Krakauer, 2008). The decision-making process intervenes when it is necessary to choose between multiple possible actions, based on value, cost, or probability of success. Action selection occurs through the integration of signals coming from the orbitofrontal cortex and basal ganglia, which evaluate the available motor options and guide the optimal choice according to goals (Redgrave, Prescott, & Gurney, 1999; Cisek & Kalaska, 2010). Emotions and motivation also directly modulate movement preparation and execution. Dopamine, for example, in addition to regulating motor tone, plays a crucial role in motivation for action, and its deficiency in extrapyramidal pathologies such as Parkinson's disease compromises the voluntary initiation of movement (Salamone & Correa, 2002). Structures such as the amygdala, in connection with the prefrontal cortex, contribute to regulating motor responses based on emotional states (LeDoux, 1996).

Finally, neuroimaging studies support the idea that movement and cognition share common neural networks, particularly in processes of meaning comprehension related to action observation and imitation. Activation of Broca's area and premotor areas during the listening of action-related words, even in the absence of linguistic production, suggests that motor representation is an integral part of language comprehension, through simulated action models (Pulvermüller et al., 2005; Hauk, Johnsrude, & Pulvermüller, 2004; Tettamanti et al., 2005).

Although locomotion is often considered an automatic and predominantly motor activity, numerous neuroscientific findings show that it is actually a highly cognitive behavior, whose efficient performance requires the dynamic integration of multiple higher mental processes. In complex environmental conditions or when locomotion is accompanied by a secondary cognitive task, the involvement of cognitive resources becomes even more marked. One of the main cognitive processes involved is attention, both selective and divided, essential for orienting in the environment, avoiding obstacles, and maintaining pace while interacting with multiple stimuli. In real situations, the ability to divide attention between motor control and other sensory or cognitive inputs is crucial to ensure movement safety and efficiency (Corbetta & Shulman, 2002; Yogev-Seligmann, Hausdorff, & Giladi, 2008). Executive functions also play a central role. Cognitive flexibility allows movements to be quickly adapted to sudden changes, while inhibitory control is necessary to suppress inappropriate or risky actions (Diamond, 2013; Aron, Robbins, & Poldrack, 2004). Moreover, continuous monitoring of locomotor behavior, supported by the prefrontal cortex, is essential to correct errors and maintain the motor goal. Working memory is involved in route planning and in managing spatial and temporal information during walking. For example, to reach a destination it is necessary to keep a spatial goal active, constantly update position relative to it, and remember any deviations (Baddeley, 2003; Fuster, 2008; Ptak, 2012). These functions are mainly mediated by the dorsolateral prefrontal cortex and its connections with the parietal system and hippocampus. Another fundamental aspect is spatial navigation, which requires the creation and use of mental representations of the environment. Humans integrate visual, vestibular, and proprioceptive information to orient themselves in space, both in reference to external landmarks (allocentric navigation) and relative to their own body position (egocentric navigation). The structures involved include the hippocampus, posterior parietal cortex, and retrosplenial cortex (Burgess, Maguire, & O'Keefe, 2002; Wolbers & Hegarty, 2010). Effective locomotion control also relies on sensorimotor anticipation processes. The brain, through internal models, is able to predict the sensory and motor consequences of an action before it happens, ensuring fluidity and stability in movement. These predictive mechanisms are supported by the cerebellum and parietal cortex, which integrate sensory and motor information in real time (Wolpert, Ghahramani, & Jordan, 1995; Shadmehr & Krakauer, 2008). At every step, the motor system must make decisions regarding the most appropriate direction, speed, and trajectory, based on environmental constraints, goals, and feedback. This motor decision-making process is supported by the basal ganglia, in interaction with the premotor cortex and the orbitofrontal cortex, which evaluate the cost and value of the different action alternatives (Cisek & Kalaska, 2010; Redgrave, Prescott, & Gurney, 1999).

Finally, locomotion depends on effective multisensory integration, which allows the nervous system to combine visual, proprioceptive, vestibular, and tactile inputs to maintain balance, regulate gait, and interact with the environment. This integration is mediated by the parietal cortex, premotor areas, and the insula, structures that contribute to building a dynamic body image and postural control (Massion, 1992; Ivanenko & Gurfinkel, 2018). In conclusion, locomotion is a behavior that reflects the joint action of sensory, motor, and cognitive systems, strongly interconnected. The intervention of cognitive processes allows the nervous system to regulate locomotion in a flexible and adaptive way, ensuring safety, efficiency, and the ability to interact with a constantly changing environment.

4.2. Visual Motion Perception

Visual Motion Perception plays a key role of the visual system's ability to decode and respond to a dynamically changing environment. Unlike static visual features such as shape or color, motion provides critical temporal information, allowing the brain to perceive ongoing events, detect threats, and guide adaptive behavior in real-time. Through this perceptual capacity, the visual system can detect moving objects, determine their trajectory, speed, and direction, and anticipate their future positions. This predictive capability is essential not only for avoiding potential dangers but also for facilitating smooth and coordinated motor actions. From an ecological perspective, motion perception likely evolved as a rapid detection system to respond to changes in the environment—such as predators, prey, or moving obstacles. Its ubiquity across species—from insects to primates—underscores its evolutionary value. In human development, sensitivity to motion emerges early, even before full acuity of form vision, suggesting that motion serves as a scaffold for later-developing visual competencies (Johnson, 2005).

Motion perception supports a range of survival-related cognitive and motor functions, including:

- Spatial orientation**:** Motion cues provide essential reference frames for estimating self-location and environmental layout, especially when other spatial cues are ambiguous or missing (Angelaki & Cullen, 2008).
- Selective attention**:** Motion acts as a salient visual feature that automatically captures attention, a phenomenon known as *attentional capture by motion* (Franconeri & Simons, 2003). Moving stimuli are prioritized in the visual hierarchy, enhancing the speed and accuracy of subsequent recognition and decision-making processes.
- Motor planning and control**:** Motion information is crucial for generating predictive models of object behavior (e.g., where a moving ball will be), allowing the motor system to preprogram and execute goal-directed movements such as catching, grasping, or avoiding (Shadmehr & Krakauer, 2008).
- Navigation**:** During locomotion, motion signals — particularly optic flow — guide egocentric navigation by informing the observer about heading direction and distance traveled (Warren & Hannon, 1988; Bremmer et al., 2002).

4.2.1. Self-Motion Perception

The ability to perceive one’s own movement through space (self-motion perception) is a fundamental function of the brain, serving as the base of spatial navigation, postural stability, and motor coordination. It enables the organism to track its own position and orientation in dynamic environments and to adapt its behavior in real time. This capacity emerges from the integration of multiple sensory modalities, including visual cues, particularly optic flow; vestibular input from the semicircular canals and otolith organs, somatosensory feedback from the skin and muscles, proprioceptive information about joint angles and body posture.

One of the key computational problems in self-motion perception is the disambiguation between motion induced by the observer's own movements (e.g., head or eye movements) and motion caused by independently moving objects in the environment. While both produce motion on the retina, only the latter reflects changes in the external world.

To resolve this ambiguity, the brain relies on specialized neurons known as “real-motion cells”. These cells are not merely sensitive to retinal motion per se but specifically tuned to detect objective, real-world motion—i.e., motion that remains after subtracting out the effects of eye or head movement (Galletti & Fattori, 2003). Such neurons have been identified in areas V6 and MST, where they play a critical role in stabilizing visual perception and differentiating between self-induced and external movement.

This function is essential not only for accurate motion perception but also for maintaining visual stability during activities like walking, running, or gaze shifts.

4.2.2. Optic Flow and Self-Motion Perception

Optic flow is the structured pattern of visual motion generated on the retina when an observer moves through a three-dimensional environment (**Fig.2**). Introduced by James J. Gibson (1950) within the framework of his ecological theory of perception, optic flow describes the dynamic transformation of the visual field due to body movement. This includes radial expansion centered around the focus of expansion during forward movement, contraction during backward motion, and spiral or shear patterns during rotational or lateral trajectories (Warren & Hannon, 1988; Royden et al., 1992). Unlike isolated object motion, optic flow is a global visual phenomenon encompassing the entire retinal image and driven by relative motion between the observer and surrounding surfaces.

This rich visual input provides the brain with critical information about heading direction, locomotor speed, object distance (via motion parallax), and the three-dimensional structure of the scene (Gibson, 1979). It serves as a perceptual foundation for egomotion—self-induced displacement through space—and supports higher-order processes such as navigation, spatial orientation, and dynamic control of locomotion (Greenlee et al., 2016; Duffy, 1998).

Fig.2: Visual representation of optic flow during forward movement through a three-dimensional environment. The arrows illustrate the apparent motion of visual elements on the retina, radiating outward from the focus of expansion.

Optic flow can arise from actual body displacement or be artificially induced in immersive contexts (**Fig.3**) such as virtual reality or treadmill-based setups. In both cases, it generates a coherent illusion of motion—known as vection—which can deceive the nervous system into experiencing a sensation of real movement (Campos et al., 2012). This makes optic flow a powerful tool for studying the neural bases of movement and simulating ecological locomotion.

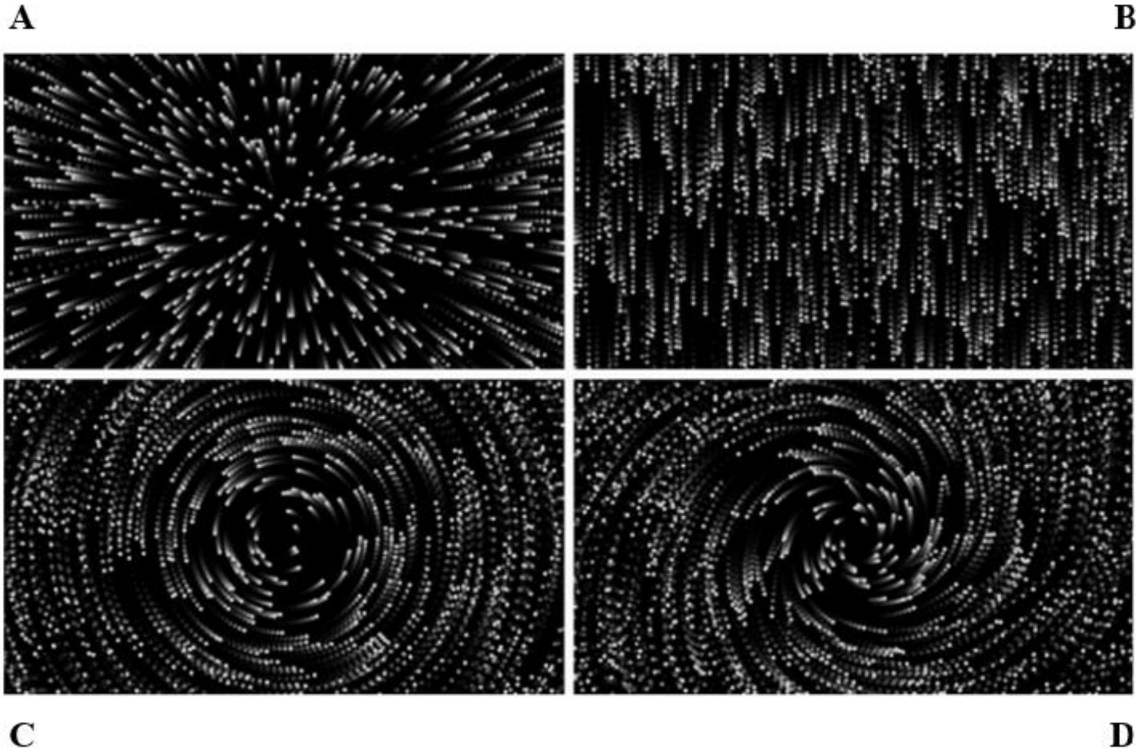


Fig.3: Examples of optic flow patterns corresponding to different types of self-motion. (A) radial expansion during forward translation; (B) vertical motion during upward translation; (C) pure rotation around the visual axis; (D) spiral optic flow combining rotation and translation. Each pattern represents global motion cues on the retina, supporting perception of direction, speed, and type of movement through the environment.

The optic flow system is crucial for numerous behavioral and cognitive functions:

- Egomotion estimation and heading control.
- Postural regulation, especially in conditions with degraded vestibular input.
- Obstacle avoidance and collision detection via looming cues.
- Visuospatial attention, anticipatory motor planning, and action programming.
- Real-time modulation of step length, speed, and trajectory in complex terrains.

Modern computational and theoretical models further underscore the significance of optic flow. Bayesian approaches suggest that the brain integrates optic flow with internal priors about motion, weighting sensory inputs by reliability to form an optimal self-motion estimate (Fetsch et al., 2009; Ernst & Bülthoff, 2004). Predictive coding frameworks propose that high-level areas (like parietal and cingulate areas) generate expectations of sensory outcomes based on movement, comparing them with actual input to adjust internal models in real time (Keller & Mrsic-Flogel, 2018).

Finally, disruptions in optic flow processing have been associated with clinical conditions such as Parkinson’s disease, vestibular dysfunctions, and spatial neglect, underscoring its fundamental role in maintaining perceptual, cognitive, and motor integrity (Karnath & Dieterich, 2006; Davidsdottir et al., 2008).

In conclusion, optic flow perception is a multisensory, computationally rich mechanism that bridges perception and action. By integrating visual, vestibular, and proprioceptive inputs, it enables the brain to generate accurate, dynamic models of self-motion, supporting orientation, navigation, postural control, and goal-directed movement in both real and simulated environments.

4.3. The egomotion areas in monkeys

Several single unit and neuroimaging studies have demonstrated that passive viewing of optic flow stimuli activates a network of higher-level motion areas. This network includes cortical regions known for being involved in the visual motion perception and well-studied through the years by several authors, like the middle superior temporal (MST) area (Saito et al. 1986; Tanaka et al. 1989; Orban et al. 1992; Duffy 1998; Vanduffel et al. 2001; De Angelis et al. 2012) and the superior temporal polysensory (STPm) area (Nelissen et al. 2006) in the superior temporal sulcus, the ventral intraparietal (VIP) area in the intraparietal sulcus (Duhamel et al. 1998), area PEc in the anterior precuneus (Raffi et al. 2002, 2011), the visual posterior Sylvian (VPS) area in the parieto-insular vestibular cortex (Chen et al. 2011a, b) and area V6 in the parieto-occipital sulcus (Galletti et al. 1996). In the following sections, I will describe in more detail three monkey regions which are particularly relevant for the studies presented in this thesis. These regions are the well-known V6 and PEc areas and the recently identified pmCSv region, in the cingulate cortex, all involved in the analysis of optic flow stimulation generated by the movement of the observer. I will describe the anatomical organization and thefunctional properties of these three regions as well as their connectivity.

4.3.1. Macaque Area V6

The cortical visual area V6 in macaques is a retinotopically organized extrastriate region (**Fig. 4**), situated in the anterior bank and fundus of the parieto-occipital sulcus (POs). This region represents the entire contralateral visual hemifield, with a distinctive emphasis on the peripheral visual field, lacking the typical cortical magnification observed in primary visual cortex and other extrastriate regions such as MT/V5.

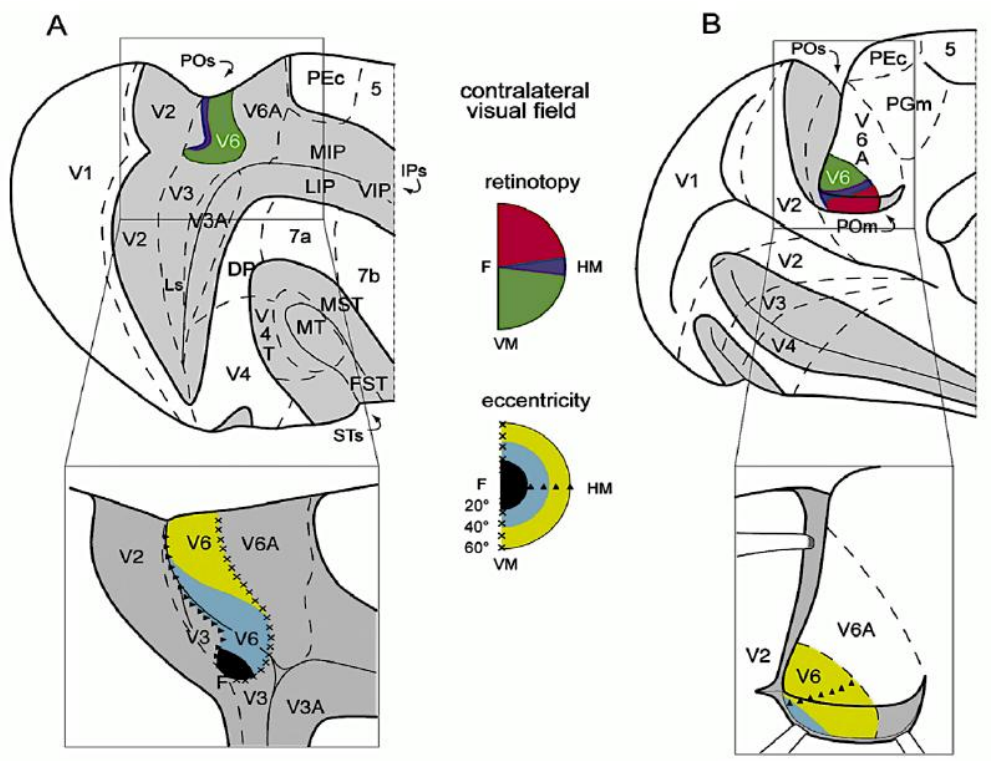


Fig.4: Retinotopic organization and cortical localization of area V6 in the macaque brain. (A) Lateral view of the left hemisphere showing the position of area V6 in relation to surrounding visual and parietal areas. (B) Medial view of the left hemisphere showing area V6 on the medial surface, adjacent to V2 and area 6M.

Electrophysiological studies have revealed that V6 neurons exhibit high selectivity for direction and velocity of motion. These neurons respond robustly to the movement of oriented borders or luminance-defined stimuli (e.g., dark-light edges or bars) across their receptive fields. The discharge of a typical direction-selective neuron is strongly modulated by motion in a preferred direction, while movement in the opposite direction results in suppression or complete silencing of activity.

Notably, V6 is populated by a specialized class of neurons known as "real-motion cells". Unlike conventional motion-sensitive cells that respond to any retinal displacement, these neurons are capable of discriminating external object motion from retinal motion induced by eye or head movements. A real-motion cell, for example, fires when a stimulus moves in space while the animal maintains fixation, but remains silent if the same retinal displacement is produced by a saccade or head rotation. This implies the integration of extraretinal information—such as efference copies or proprioceptive signals—to isolate real-world motion from self-induced motion cues.

V6 receives direct afferents from early visual areas including V1, V2, V3, and V3A, and in turn sends projections along two major output streams (**Fig.5**):

- A lateral pathway targeting dorsal extrastriate areas such as MT, MST, V4T, and LIP,
- A medial pathway projecting to bimodal visuo-somatosensory regions like V6A, MIP, and VIP.

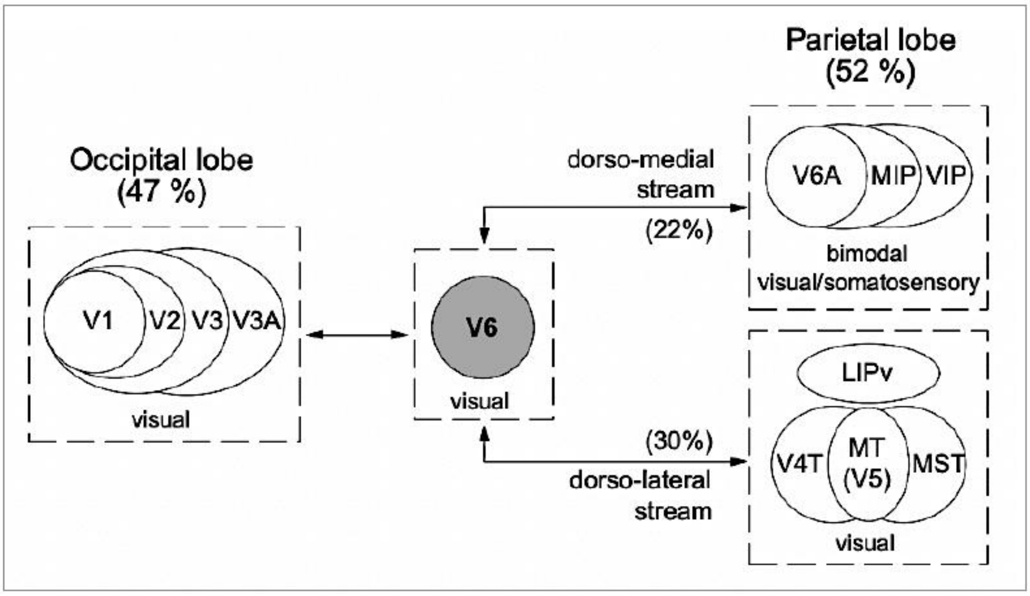


Fig.5: Schematic representation of visual processing pathways involving area V6 in the macaque brain. The diagram shows the flow of visual information from early visual areas in the occipital lobe (V1, V2, V3, V3A;) to area V6, and from V6 to regions in the parietal lobe.

This anatomical organization situates V6 as an early-stage processor of motion information within the dorsomedial visual stream. Its outputs are relayed to higher-level regions involved in visuomotor integration, reaching, and navigation, consistent with its presumed role in supporting vision-for-action computations. An evidence that this area the same function of V6 areas in humans derives from Pitzalis et al. (2021), who demonstrated an activation induced by a simulated optic flow in primates in this region (**Fig. 6**).

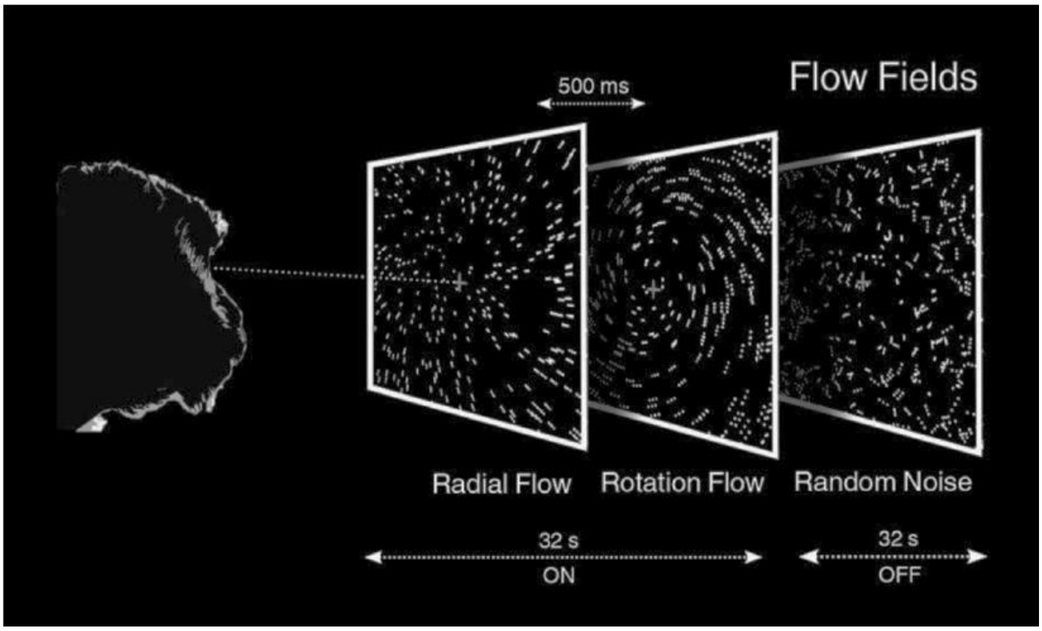


Fig.6: Visual motion stimuli used to activate motion-sensitive brain areas in primates. Schematic of the flow field paradigm presented to a primate subject.

Despite initial assumptions that V6's role in optic flow processing was marginal compared to MST, recent macaque studies challenge this view. Using virtual reality-based paradigms, Fan et al. (2015) demonstrated that V6 neurons show reliable and fine-grained tuning to heading direction, including the ability to discriminate subtle deviations from forward or backward motion. This makes V6 a significant contributor to egomotion perception based on visual cues alone.

V6 exhibits a precise visuotopic map, representing the visual field in a continuous, point-to-point manner. Interestingly, its peripheral emphasis, particularly in the lower visual field, aligns with behavioral relevance, given that peripersonal space below the line of sight is critical for locomotion and interaction with the ground plane.

In conclusion, area V6 in macaques is a crucial node within the dorsal visual network, characterized by:

- Strong direction and motion selectivity, including real-motion sensitivity,
- Broad-field retinotopy with emphasis on the periphery,
- Multistage connectivity to both early visual and higher-order visuomotor areas,
- Participation in optic flow and heading perception, particularly in the visual domain.

Through these properties, V6 contributes significantly to visual motion analysis and spatial orientation, laying the groundwork for action planning and sensorimotor integration in dynamic, real-world contexts.

4.3.2. Macaque Area PEc

Area PEc, located in the posterior segment of the superior parietal lobule (SPL) on the medial wall of the intraparietal sulcus, is a key region within the macaque posterior parietal cortex (PPC). Anatomically distinct from its anterior neighbor PE, PEc is typically associated with Brodmann area 7, and is functionally integrated within the dorsomedial parietal network alongside V6A and PGm, contributing to whole-body orientation and visually guided locomotion (Galletti et al., 1996; Bakola et al., 2010; Gamberini et al., 2021).

Unlike primary somatosensory areas that show clear somatotopic organization, PEc neurons display a distributed and overlapping representation of multiple body segments, including responses to passive joint manipulation of the hips, shoulders, knees, and feet. This distributed encoding is consistent with a functional role in integrating posture-related information from different body parts (Breveglieri et al., 2006; Gamberini et al., 2021).

Functionally, PEc contains at least three types of neurons: (1) somatosensory unimodal neurons, responsive to passive body stimulation; (2) visual unimodal neurons, sensitive to motion direction, stimulus speed, and edge orientation; and (3) a large subset of bimodal visuo-somatosensory neurons, which form the basis for multisensory integration during locomotion and posture control (Breveglieri et al., 2008; Di Marco et al., 2021).

One of the most relevant findings regarding PEc's visual specialization concerns its sensitivity to wide-field optic flow patterns, especially those that simulate egomotion, such as radial expansion (forward motion) and contraction (backward motion). Single-neuron recordings have revealed PEc neurons' preference for specific focus of expansion (FoE) positions, and their responses are modulated by eye position and trajectory curvature, suggesting a role in computing dynamic self-motion vectors (Gamberini et al., 2021; Di Marco et al., 2021).

Interestingly, in many bimodal PEc neurons, the visual and somatosensory receptive fields are spatially non-coincident—for example, a neuron might respond visually to stimuli near the shoulders while being somatosensorily tuned to the legs. This suggests that PEc does not simply integrate co-localized stimuli but instead contributes to a holistic representation of body-in-space relationships, crucial for whole-body spatial orientation and real-time adjustment during movement (Breveglieri et al., 2008; Gamberini et al., 2021).

From a connectivity perspective (**Fig. 7**), PEc receives visual input from area V6A, proprioceptive input from somatosensory regions, and projects to premotor and cingulate motor areas, including area F2 and cingulate areas 23 and 24d, which are involved in voluntary motor control (Galletti et al., 2001; Bakola et al., 2010). Importantly, PEc is also connected with vestibular-related cortices, such as the parieto-insular vestibular cortex (PIVC) and the posterior insula, and receives afferents from the posterior claustrum, which is implicated in high-level multisensory integration (Gamberini et al., 2021; Di Marco et al., 2021).

Altogether, these anatomical and functional properties position PEc as a multisensory integration hub, playing a critical role in supporting visually guided locomotion, postural control, and egocentric spatial orientation. Its ability to flexibly combine optic flow, proprioception, and vestibular cues enables macaques to adapt their body schema and heading during complex navigation tasks in naturalistic environments.

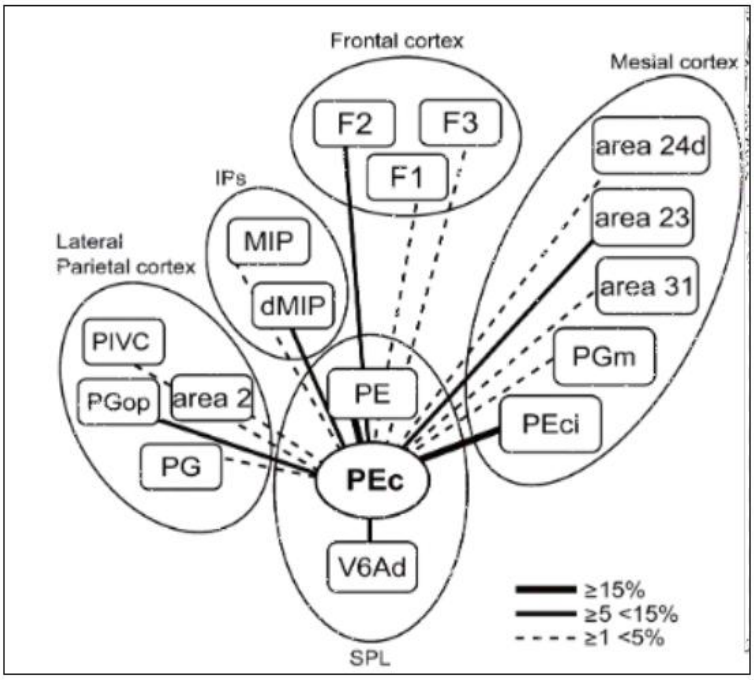


Fig. 7: Cortical connectivity of area PEc in the macaque brain.
Schematic diagram showing the major cortical afferents to area PEc, located in the superior parietal lobule (SPL). PEc receives inputs from multiple regions across the lateral parietal, frontal, and mesial cortices.

4.3.3. Macaque area pmCSv: : A Multisensory Node for Egomotion-Related Processing

The putative macaque CSv (pmCSv) represents a candidate homolog of the cingulate sulcus visual area (CSv) well-established in humans. Although single-neuron electrophysiological evidence for a macaque CSv remains limited—likely due to the technical challenges of accessing deep cingulate sulcus structures—recent functional neuroimaging studies have identified a small region within the posterior cingulate cortex of macaques that responds selectively to optic flow patterns consistent with self-motion. This region, situated within Brodmann area 23, was designated pmCSv by Cottereau and colleagues (2017), who demonstrated its nearly exclusive responsiveness to visual stimuli simulating forward locomotion

The functional profile of pmCSv suggests a specialized role in the detection of egomotion-related visual cues. Unlike lower-tier motion areas such as MT or MST, which process local or intermediate flow fields, pmCSv appears to integrate higher-order optic flow patterns that signal global self-displacement. This aligns with findings from analogous human CSv studies, where the area showed strong selectivity for coherent, self-motion-compatible flow fields over scrambled or object-motion stimuli

From a connectomic perspective, pmCSv exhibits robust structural and functional connectivity with a broad array of regions involved in multisensory integration and spatial navigation. These include visual-vestibular areas such as VIP, VPS, and MSTd, all of which encode congruent optic flow and inertial signals related to heading and motion (Gu et al., 2008; Chen et al., 2011). Additionally, pmCSv projects to and receives input from motor-related cingulate areas—notably the ventral and rostral cingulate motor areas (CMAv and CMAr) and the supplementary motor area (SMA/F3)—indicating a possible role in coupling visual perception of self-motion with motor output for navigation and balance

Intriguingly, pmCSv also shows strong reciprocal connections with the medial parietal cortex, including area 7m/PGm, a region known for its involvement in eye and hand movement planning and its projection to V6A, PEc, and other visuomotor transformation hubs. These connections further support the hypothesis that pmCSv may function as a sensorimotor interface, translating egocentric visual motion information into behaviorally relevant motor commands

Moreover, pmCSv's connectivity extends to the caudal superior temporal polysensory area (cSTP), which is known to process integrated visual and somatosensory information, reinforcing its putative role as a multisensory hub. Its links with primary and secondary somatosensory areas (e.g., areas 1 and 3) suggest additional access to proprioceptive and tactile feedback during active locomotion

Taken together, the pmCSv in macaques emerges as a compelling candidate for a cingulate-based egomotion-processing center, functionally positioned at the crossroads of visual motion analysis, vestibular integration, and motor control. While invasive recordings are still needed to directly characterize its neural dynamics, existing fMRI and tract-tracing studies support its classification as a core component of the egomotion network in non-human primates.

4.4. Neural Basis of Egomotion in Humans

4.4.1. Egomotion-Related Regions Responding to the Flow Fields Stimulus

Egomotion refers to the visual perception of self-motion through the environment, and it is primarily supported by optic flow: a coherent pattern of visual motion across the retina that arises as an individual moves forward, backward, or along curved paths. This visual input enables the brain to estimate heading direction, anticipate environmental changes, and plan movements accordingly. Among the most robust experimental stimulus used to study this process is the Flow Fields stimulus developed by Pitzalis et al. (2010), which simulates complex patterns of optic flow mimicking real-world visual conditions during locomotion (**Fig. 8**).

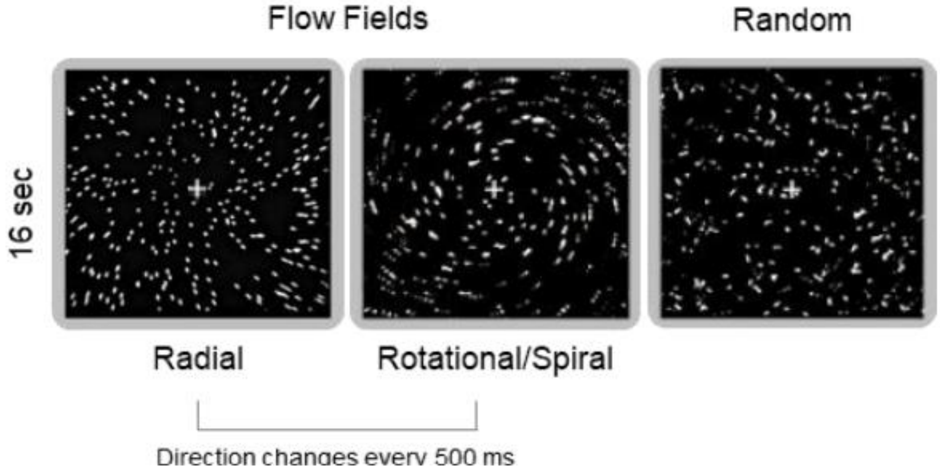


Fig.8: Examples of visual stimuli used in the experiment to simulate different types of motion. Three flow field conditions are shown: Radial, Rotational/Spiral, and Random motion. Each stimulus lasts 16 seconds, with motion direction changing every 500 milliseconds. These stimuli are used to study how the brain processes optic flow and self-motion cues.

Neuroimaging studies employing this stimulus have consistently identified a core set of cortical regions activated in response to egomotion-compatible optic flow: V6+, pIPS/V3A, VIP/IPSmot, CSv, pCi, and PIC. These regions form a distributed network across occipital, parietal, cingulate, and insular cortices (**Fig. 9**).

The V6+ complex, located within the dorsal portion of the parieto-occipital sulcus, includes both the retinotopically defined area V6 and the anteriorly adjacent V6Av. This region shows high sensitivity to translational optic flow and plays a crucial role in depth estimation via motion parallax. The precise encoding of heading and environmental layout makes V6+ particularly suited for planning navigation in dynamic visual environments.

The pIPS/V3A region lies within the posterior intraparietal sulcus and is involved in visual motion processing related to scene structure and three-dimensional spatial layout. It contributes to object and background segmentation during motion, essential for recognizing obstacles and navigating complex environments.

IPSmot/VIP, located in the ventral intraparietal sulcus, is a multimodal hub that integrates visual, vestibular, and somatosensory signals. It shows strong selectivity for optic flow patterns consistent with self-motion, particularly when accompanied by cues of head or body movement, and encodes egomotion in body-centered coordinates. This integration makes it essential for heading perception, postural stability, and the planning of locomotor actions in complex and dynamic environments.

CSv (cingulate sulcus visual area) and pCi (posterior cingulate area) are medial parietal regions that exhibit strong selectivity for coherent optic flow consistent with self-motion. These regions display a preference for optic flow patterns that simulate curved versus straight paths and forward versus backward movements, suggesting a specialization in analyzing complex trajectory dynamics.

PIC (posterior insular cortex), known for integrating multisensory inputs, responds to both visual and vestibular signals, positioning it as a crucial interface for integrating internally and externally generated motion cues.

Together, these regions constitute a specialized visual network that detects, interprets, and contextualizes motion cues necessary for the perception of self-motion, orientation, and spatial navigation.

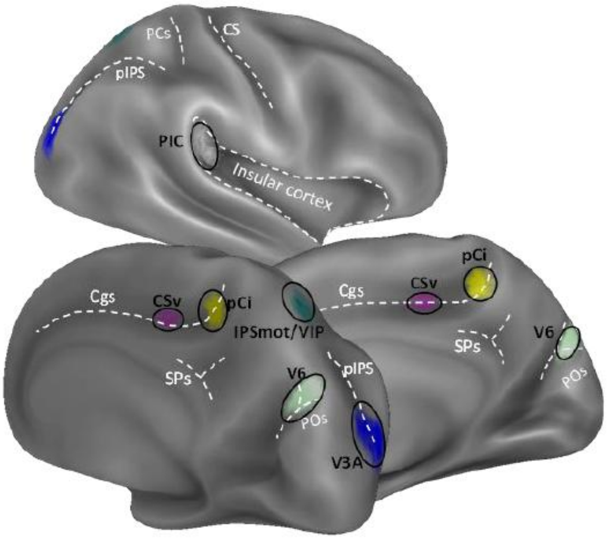


Fig. 9: Brain regions involved in processing optic flow and self-motion perception. Highlighted areas include visual and multisensory regions such as V6, V3A, pIPS, POS, CSv, VIP, and PIC, distributed

across parietal, occipital, and insular cortices. These regions integrate visual motion cues to support egomotion, spatial orientation, and navigation.

4.4.2. Motor Properties of Egomotion-Related Regions

Beyond their well-established visual roles, several egomotion-related regions also participate in motor functions. Serra et al. 2019 tested the sensitivity of V6+, pIPS/V3A, IPSmot/VIP, pCi, Csv and PIC to a pure motor task (**Fig. 11**) requiring to actively perform long-range arm and leg movements. Specifically, they tested whether these regions involved in processing optic flow signals simulating self-motion are also activated by active lower limb movements, and hence are likely involved in guiding human locomotion. Authors found that pCi, PIC, and CSv (visuomotor areas) responded to leg movements, whereas V6+, V3A, and VIP (visual areas) did not, and the pattern of functional cortical connections of these areas was consistent with its role in the motor control of leg movements (**Fig. 10**). Specifically, the connections of the three visuomotor regions extend to the medial portion the primary somatosensory and motor cortices, where the sensory and motor inputs coming from the legs and feet are more represented (Zlatkina, Amiez, & Petrides, 2016; Akselrod et al. 2017; Tal, Geva, & Amedi, 2017; Chen, Kreutz-Delgado, Sereno, & Huang, 2017). In addition to somatomotor connections, pCi, PIC, and CSv are also connected with peripheral early visual areas V1–V2 and with the insular cortex and the posterior part of the perisylvian cortex, which likely includes the PIVC known to be the potential hub of the cortical vestibular network (Frank, Sun, et al. 2016; Frank, Wirth, et al. 2016). This implies that pCi, PIC, and CSv provide sensory information to the motor system for use in guiding whole-body movements. The combined response of these areas to optic flow and leg movements supports the hypothesis that these regions are primarily involved in all classes of actions occurring during self-motion such as walking, running, or stepping. Overall, this study demonstrated for the first time a functional subdivision of the six visual areas, in which the more posterior V6+, V3A, and IPS-mot/VIP (not responding to leg and without connections with the somatomotor cortices) seem to be primarily engaged in the visual processing of egomotion retinal components, which is required to coordinate eye, arm, and body motions while navigating in a complex and dynamic environment. Instead, the most anterior areas, pCi, PIC, and CSv (responding to leg and with connections with the somatomotor cortices), are likely to play a motor function in egomotion signal processing, assessing somatomotor input from the lower limbs, together with visual egomotion signal to control locomotion. CSv, for instance, is hypothesized to contribute to the real-time adjustment of gait and posture by mapping visual motion cues onto motor commands, especially when changing direction during walking. Interestingly, other regions such as V6+ and pIPS/V3A do not exhibit significant motor-related responses, highlighting a functional segregation between strictly visual and visuo-motor components of the egomotion network.

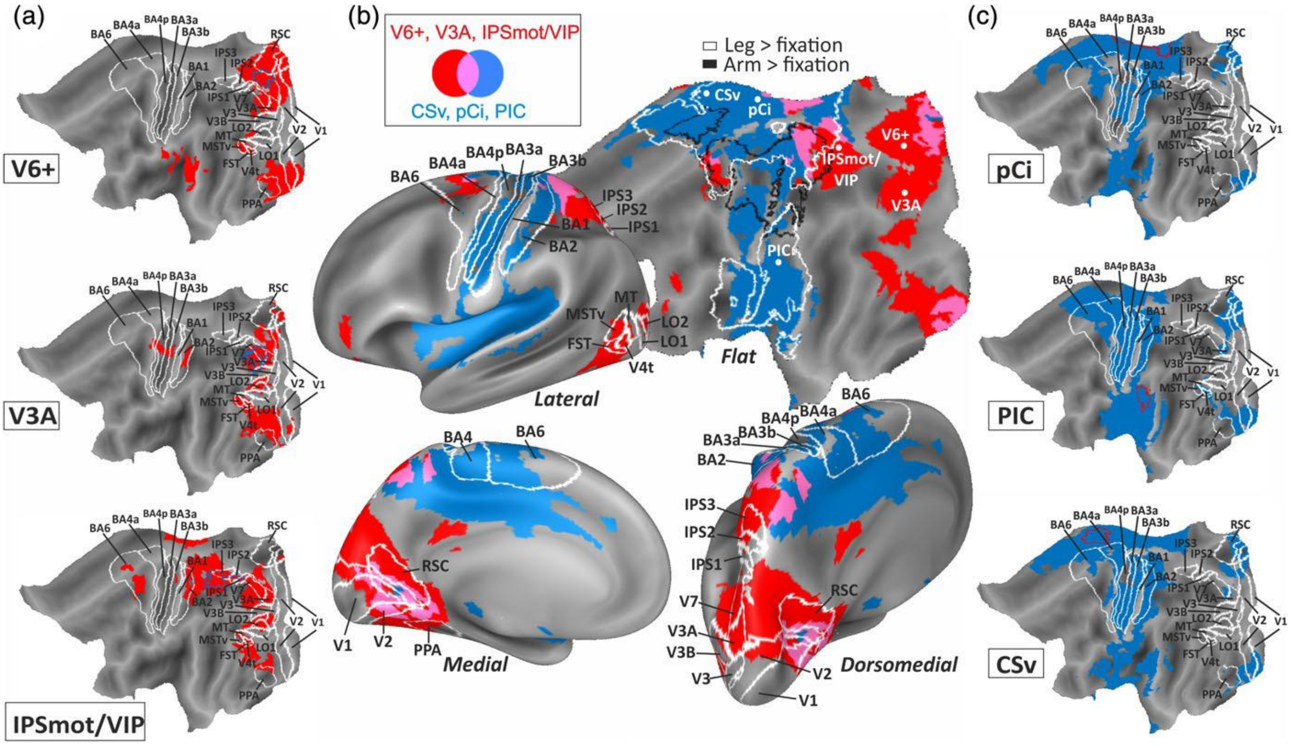


Fig. 10. Functional connectivity maps of egomotion-related ROIs. Functional connectivity maps associated with the three seed visual regions (a, blue color outlined over red patches) and the three seed visuomotor regions (b, red color-outlined over blue patches) superimposed over flatted representation of the left hemisphere of Conte69 surface-based atlas. The borders of previously identified areas (Brodmann, 1909/1925; Kolster et al., 2010; Sulpizio, Committeri, Lambrey, Berthoz, & Galati, 2013; Van Essen, Glasser, Dierker, Harwell, & Coalson, 2011) are outlined in white (see the Methods section for details). (c) Overlap of two functional connectivity maps, one associated with the group of ROIs not responding to leg movements (visual areas, red patches) and the other associated with the group of ROIs responding to leg movements (visuomotor areas, cyan patches). Light purple patches represent overlapping pattern between the two maps and reflect shared connections. Connectivity maps are superimposed over the flattened and inflated (lateral, dorsomedial, and medial views) representation of the left hemisphere of Conte69 surface-based atlas. The borders of previously identified areas (Brodmann, 1909/1925; Kolster et al., 2010; Sulpizio et al., 2013; Van Essen et al., 2011) are outlined in white (see the Methods section for details). In the flat map, the white and black outlines indicate the cortical network activated by the leg > fixation and arm > fixation contrasts, respectively. The centers of mass of V6+, V3A IPSmot/VIP, pCi, PIC, and CSv are marked by a white spot. CSv, cingulate visual area; IPSmot/VIP intraparietal motion area/ventral intraparietal; pCi, posterior cingulate sulcus area; PIC, posterior insular cortex; ROI, region of interest; V6+, V6 complex. From Serra et al. 2019

4.4.3. Leg-Related Somatomotor Regions Responding to the Flow Fields Stimulus

Recently, in addition to these egomotion regions, activation in response to visual optic flow, was observed also in the precuneus, in correspondence of a cortical territory where the human homologues of areas PEc and PE were recently found, immediately posterior to the medial portion of S-I representing the lower limbs. These regions were identified using for the first time an innovative set-up (**Fig. 11**) to perform a leg movement in MRI.

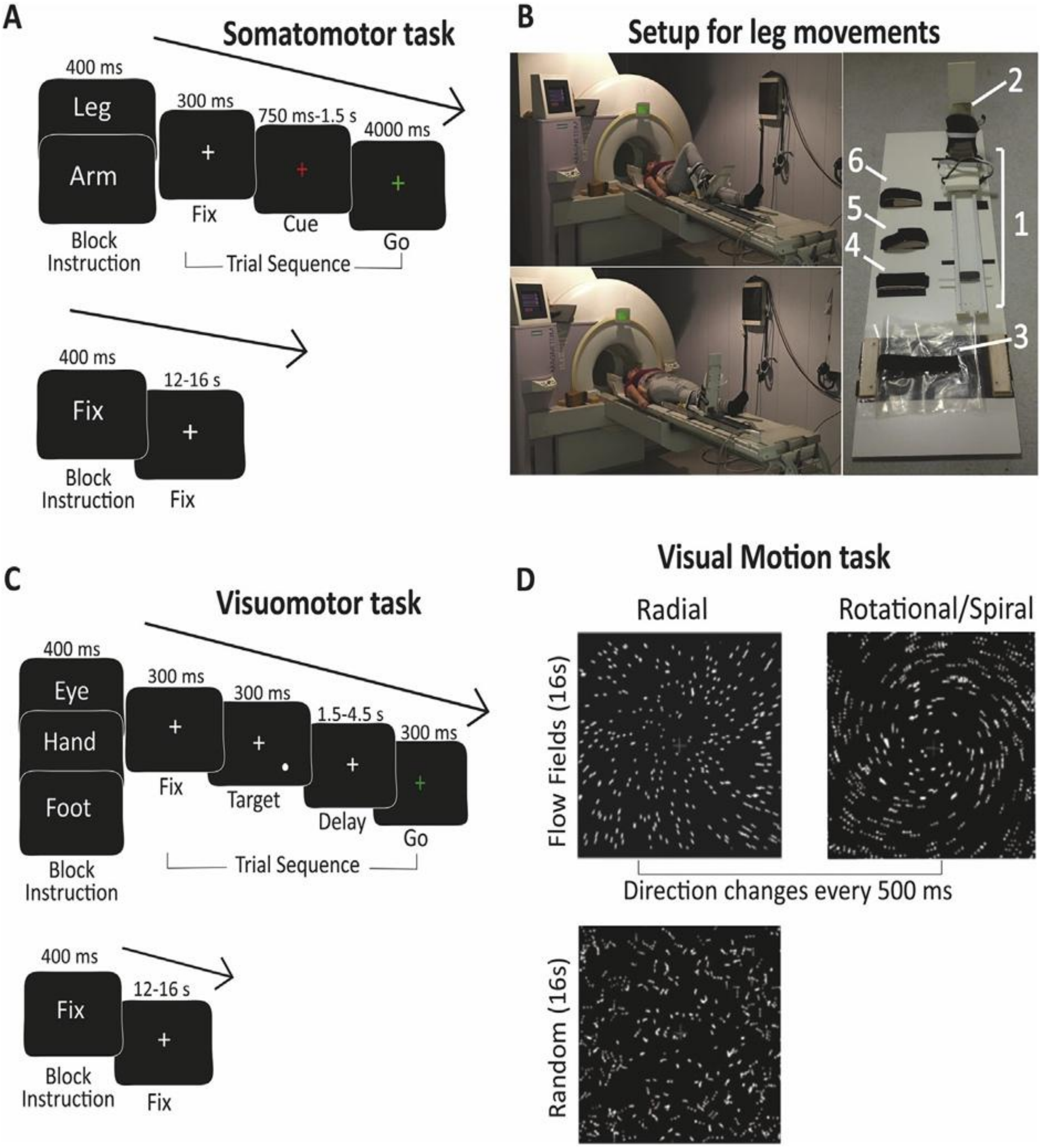


Fig. 11; set-up for leg movements. It consisted of an aluminum track fixed via Velcro straps on a wooden table which perfectly fitted the scanner bed. Subjects laid down on the wooden table, with their right leg extended along an aluminumtrack (1) and with their right foot comfortably fixed with elastic straps to an aluminum support (2) which sliding along the track allowed subjects to perform fluid and controlled long-range leg flexion and extension. Velcro straps for immobilizing hip (3), tight (4), knee (5) ankle (6) of the left leg controlled for whole-body movements. Importantly,

Specifically, authors used a somatomotor task requiring subjects to perform a longrange leg movement, designed to maximally stimulate limb joints in order to maximally activate the somatomotor cells located in this area (which in macaques is highly sensitive to passive joints manipulation). This movement consisted of rightward rotation of the right leg followed by leg flexion and subsequent leftward rotation of the right leg followed by leg extension to return at the initial resting position. The term “somato-motor” is adopted because in the task used to map these regions, we used a longrange leg movement which recruits several muscles at the same time and the three main joints of the leg (i.e., ankle, knee, and hip) as well as significant somatosensory feedbacks. By using this somatomotor task, Pitzalis and coworkers (2019) were able to map three areas responding to leg movements (**Fig. 12**):

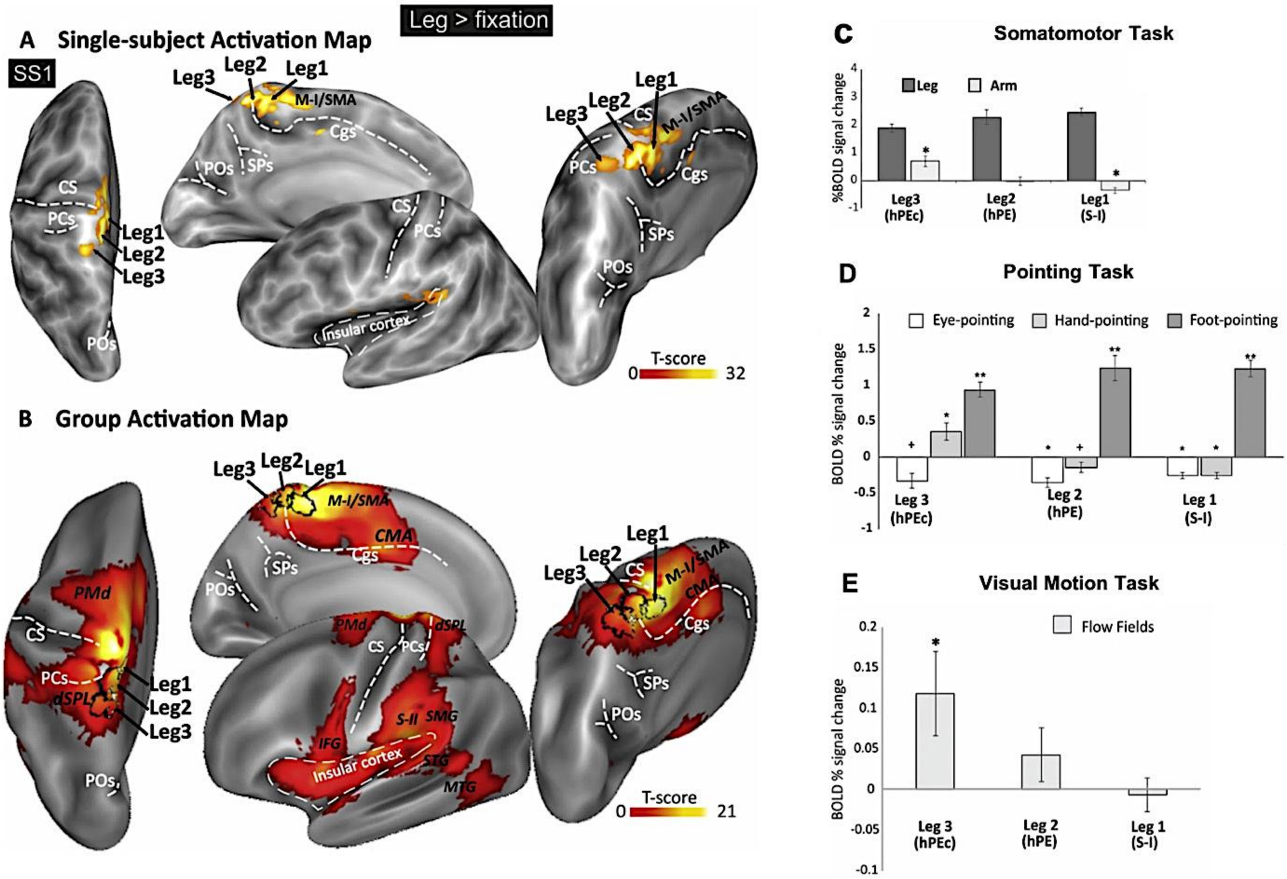


Fig. 12: Three leg-related regions. (A-B) Three leg-related regions from the Somatomotor task: functional activation maps in the contrast “Leg>Fixation”. (A) Single subject activation map displayed on the cortical surface reconstruction of the left hemisphere of a representative subject (SS1). (B) Group activation map displayed on the left hemisphere of the Conte69 atlas brain. In A and B, activation maps are rendered in superior, medial, lateral and dorsomedial views. Areas more active during leg movements are labelled: M-I, primary motor cortex; SMA, supplementary motor area; CMA, cingulate motor area; dSPL, dorsal superior parietal lobule; PMd, dorsal premotor area; SMG, supra-marginal gyrus; S-II, secondary somatosensory cortex; STG, superior temporal gyrus; IFG, inferior frontal gyrus; MTG, middle temporal gyrus. Light and dark grey respectively represents gyri and sulci. The fundus of main sulci is indicated using dotted line and labelled as follow: POs, parieto-occipital sulcus; PCs, postcentral sulcus; CS, central Sulcus; SPs, sub-parietal sulcus; Cgs, cingulate sulcus. The color scale in A and B indicates the statistical significance of the activations using the FDR corrected p-values. (C) Somatomotor task: arm-related responses within the three leg-related regions. Plots show parameter estimates in each leg-related region for the leg (dark grey) and arm (light grey) conditions. Asterisks refer to T-test versus zero. *$p < 0.001$. (D) Visuomotor task: hand and foot pointing related responses within the three leg-related regions. Plots for each region indicates the averaged BOLD percent signal change standard error of the mean across subjects for each experimental condition: Eye-pointing (white), hand-pointing (light grey), foot-pointing (dark grey). Asterisks refer to T-test versus zero. **$p < 106$; *$p < 0.001$; t$p < 0.05$, Bonferroni-uncorrected. (E) Visual task: visual motion related responses within the three leg-related regions. Plots for each region indicates the averaged BOLD percent signal change standard error of the mean across subjects for Flow Field blocks (relative to random motion). Asterisks refer to T-test versus zero. *p 1⁄4 0.02. Modified from Pitzalis et al. (2019)

Key among these is hPEc (the human homologue of macaque PEc), hPE, and S-I (primary somatosensory cortex). These regions were identified via task-based fMRI paradigms involving long-range cyclical leg movements. Notably, hPEc is situated in the anterior superior parietal lobule, a region with demonstrated sensitivity to both somatosensory and visual input.

hPEc displayed a unique response pattern: it was particularly activated during incongruent visuomotor conditions, such as when visual optic flow indicated motion in one direction while the executed leg movement proceeded in another. This suggests a role in sensorimotor conflict detection, allowing the system to identify mismatches between expected and actual sensory feedback—a function critical for maintaining accurate motor control in dynamic environments.

By contrast, hPE and S-I exhibited robust activation in response to both visual and motor tasks, but without evidence of integration. This implies that while these areas receive both types of input, they may process them in a parallel rather than integrative manner.

These findings support a hierarchical processing model, wherein primary somatosensory regions like S-I contribute to low-level sensory encoding, while associative parietal regions such as hPEc function as convergence zones integrating multimodal inputs for adaptive motor control.

4.5. Multisensory Integration in Regions Responding to Visual and Somatomotor Locomotion Signals

The ability to navigate effectively through dynamic environments depends not only on isolated visual or somatosensory processing but also on the brain's capacity to integrate these inputs into a coherent perceptual and motor framework. Multisensory integration enables rapid adjustments to ongoing actions, especially during complex tasks such as changing direction while walking.

To investigate this integrative capacity, Di Marco et al. (2021) designed an fMR-adaptation experiment using a factorial design that varied congruency (match/mismatch) and repetition (same/different) of visual and motor signals. Participants performed stepping movements in lateral directions while observing radial optic flow simulating congruent or incongruent heading changes. This design allowed the researchers to probe the sensitivity of different brain regions to multisensory correspondence and novelty (see **Fig. 13**).

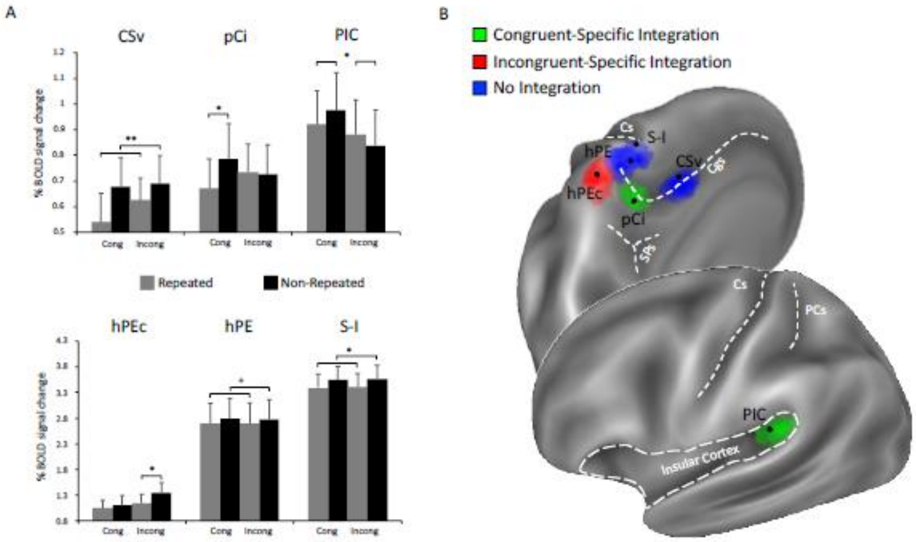


Fig. 13: A) Bar plots showing % BOLD signal change in various brain regions in response to congruent (Cong) and incongruent (Incong) motion-vestibular stimulation, under repeated and non-repeated conditions. Significant differences are indicated by asterisks (*p < .05; **p < .01), revealing distinct integration patterns across regions.
B) Surface map of the human brain highlighting regions involved in multisensory integration. Green indicates areas showing congruent-specific integration (e.g., PIC), red indicates incongruent-specific integration (e.g., hPEc), and blue indicates no integration (e.g., CSv). This mapping illustrates spatially distinct processing of vestibular-visual congruency.

Results revealed a clear functional dissociation among cortical areas. Regions like hPEc, PIC, and pCi showed congruency-dependent adaptation effects, indicating true multisensory integration. In contrast, hPE, S-I, and CSv demonstrated response adaptation irrespective of congruency, implying unimodal or parallel processing.

hPEc exhibited increased activation during incongruent visuo-motor conditions, suggesting its function as an error-monitoring node. This region may act to detect sensorimotor mismatches and relay corrective signals to motor execution systems. Such a mechanism is essential when navigating unfamiliar or unpredictable terrains.

Conversely, pCi and PIC displayed preferential responses to congruent trials. Their activation patterns suggest a role in enhancing sensorimotor coordination when visual and motor inputs are aligned, possibly facilitating more stable and efficient locomotor output.

These distinctions align with known anatomical pathways. hPEc connects with dorsal visual areas and somatosensory cortices, supporting its role in sensorimotor transformation. PIC’s connectivity with vestibular nuclei and insular regions positions it as a key hub for body motion perception. Meanwhile, pCi’s projections to cingulate motor areas highlight its contribution to voluntary movement adjustments.

Overall, the findings emphasize a distributed network of multisensory convergence regions, each specialized for distinct computational goals—whether it be sensory fusion for stable motion, detection of incongruencies, or real-time behavioral correction. These results deepen our understanding of how the human brain integrates optic flow and proprioceptive feedback to maintain locomotor control and suggest clinical relevance for rehabilitative strategies targeting these pathways in patients with balance or gait disorders.

4.5.1. The Revisited Dorsal Visual Stream

Understanding the functional architecture of the visual system has long been a central focus in neuroscience. Traditionally, visual processing was conceptualized along two main cortical pathways: the ventral stream, which supports object identification ("what"), and the dorsal stream, dedicated to spatial localization and action guidance ("where/how") (Ungerleider & Mishkin, 1982; Goodale & Milner, 1992). However, more recent evidence has led to a refinement of this model, particularly regarding the dorsal stream, which is now recognized as a heterogeneous and functionally specialized network. This "revisited" dorsal stream consists of at least two partially segregated but interacting substreams: the dorso-lateral and dorso-medial pathways (Rizzolatti & Matelli, 2003; Gamberini et al., 2021).

4.5.1.1. The Dorso-Lateral Visual Stream: Specialized for Visual Motion Analysis

The dorso-lateral stream, extending from early visual areas through MT/V5 and progressing into the lateral intraparietal sulcus (LIP), MST, and parts of VIP, is primarily concerned with the detection and analysis of visual motion. This pathway is responsible for extracting key motion parameters such as speed, direction, and pattern coherence, which are crucial for perceptual stability and navigation in dynamic environments (Born & Bradley, 2005).

Area MT/V5 serves as the core motion processing hub within this stream. It is highly sensitive to linear motion and encodes both the speed and direction of moving stimuli. Neurons in MT are direction-selective and retinotopically organized, providing a detailed map of motion in the visual field. MT projects to MST, where neurons integrate large-field motion signals and are responsive to more complex flow patterns such as expansion, rotation, and translation (Duffy & Wurtz, 1991; Britten, 2008). MST is particularly important for interpreting optic flow, the global pattern of motion experienced during self-movement. Recent work by Layton and Steinmetz (2024) using biologically constrained neural network models has provided compelling evidence that MST-like optic flow encoding may reflect sparse, non-negative coding principles, a strategy that may enhance efficiency and stability in the brain’s motion representations.

Further along the dorso-lateral trajectory, area VIP integrates visual motion with vestibular and somatosensory cues, enabling the estimation of head-centered motion and contributing to multisensory spatial representation (Bremmer et al., 2002). This region plays a critical role in detecting and reacting to external motion stimuli, particularly in peripersonal space. LIP, another dorsolateral region, supports attentional selection and eye movement planning based on visual motion input (Andersen et al., 1997). It acts as a sensorimotor interface, linking motion perception to saccadic decision-making.

Recent neurocomputational models support this hierarchical functional segregation. For example, Choi et al. (2023) introduced a dual convolutional neural network (WhereCNN/WhatCNN) to model dorsal vs. ventral stream functions, showing that WhereCNN spontaneously learns egocentric motion information similar to human eye-movement behavior and dorsal stream activations.

Collectively, the dorso-lateral stream supports perceptual functions essential for scene analysis, object tracking, spatial orientation, and preparation for eye or body movements. It transforms motion-based visual information into perceptual constructs necessary for environmental awareness and anticipatory behavior.

4.5.1.2. The Dorso-Medial Visual Stream: Vision for Action

In contrast to the perceptually driven dorso-lateral stream, the dorso-medial stream is predominantly geared toward the transformation of visual input into motor output. This pathway originates from areas V6 and V6A in the parieto-occipital region and projects medially to regions such as MIP (medial intraparietal area), PEc, and the dorsal premotor cortex (PMd). This stream is commonly referred to as the "vision-for-action" system, emphasizing its role in coordinating visually guided movements, particularly those involving the upper and lower limbs (Galletti & Fattori, 2018).

Area V6, located in the dorsal anterior bank of the parieto-occipital sulcus, processes wide-field visual motion and is specialized for encoding motion in peripheral vision. It contains a dense population of motion-sensitive neurons, including "real-motion cells" that distinguish between object motion and retinal slip caused by self-movement (Galletti et al., 1996; Galletti & Fattori, 2003). V6 projects to V6A, an adjacent area involved in visuomotor transformation. V6A is responsive to both visual and somatosensory input and is activated during reaching and grasping tasks. Its neurons encode the direction, amplitude, and endpoint of limb trajectories, often in body- or gaze-centered reference frames (Fattori et al., 2001; Hadjidimitrakis et al., 2015).

More recent studies (Sulpizio et al., 2024) using meta-analytic tools have highlighted the anterior precuneus and dorsal POS as key regions activated by both optic flow and egocentric navigation, reinforcing the idea that the dorso-medial stream is deeply involved in both self-motion perception and its motor implementation.

Downstream, area MIP receives input from V6A and contributes to arm movement planning in three-dimensional space. It integrates visual, proprioceptive, and effector-specific signals, playing a crucial role in the sensorimotor transformation required for targeted reaching and locomotor coordination (Andersen & Cui, 2009). PEc, located more caudally, is also sensitive to limb motion and participates in integrating visual motion cues with proprioceptive input from the legs. This makes it particularly relevant for gait control and navigation across complex terrain (Breveglieri et al., 2008; Gamberini et al., 2018).

At the cortical frontier of the dorso-medial stream lies PMd, which is involved in the preparation and execution of voluntary movements. PMd receives converging input from MIP and other parietal areas and is essential for selecting motor programs based on visual goals. It supports not only reaching but also more abstract motor intentions, such as planning trajectories and predicting the consequences of movement (Wise et al., 1997).

4.5.2. Functional Interaction and Integration

While the dorso-lateral and dorso-medial streams serve different functional imperatives—perception and action, respectively—they are not strictly isolated. Rather, they exhibit extensive anatomical and functional cross-talk. This interaction ensures that visual motion analysis can be seamlessly translated into goal-directed action. For instance, information processed in MST about optic flow can inform V6A and MIP about movement dynamics, aiding in postural adjustments or re-calibration of limb trajectories (Fan et al., 2015; Pitzalis et al., 2021).

Moreover, regions such as VIP and PEc act as integrative hubs where vestibular, visual, and somatosensory information converge. These areas enable the system to compute head and body position relative to external visual cues, which is indispensable for stable locomotion and balance (Bremmer et al., 2001; Bakola et al., 2010).

The dual-stream architecture allows for parallel processing of visual information for perception and action, increasing the efficiency and adaptability of the visuomotor system. Such integration may be evolutionarily optimized to support complex behaviors such as bipedal locomotion and tool use.

4.5.3. Conclusions

The revisited dorsal visual stream is best understood as a dual-network system, with a dorsolateral pathway specialized for the perceptual analysis of motion and spatial cues, and a dorsomedial pathway dedicated to translating these cues into motor behavior. This conceptual refinement bridges the gap between traditional sensory-motor dichotomies, highlighting the brain's capacity for dynamic integration of sensory input with action planning. Understanding these pathways in detail not only informs basic neuroscience but also has implications for clinical approaches to motor and perceptual disorders, and for the design of advanced prosthetic and robotic systems that emulate human visuomotor capabilities. Computational and meta-analytic approaches (Choi et al., 2023; Sulpizio et al., 2024) further confirm the functional and anatomical robustness of this model, offering powerful tools to explore and simulate the dorsal stream’s contributions to perception and action.

5. Electroencephalogram and event-related potentials

Electroencephalography (EEG) is a non-invasive technique that allows the recording of bioelectrical brain activity through the application of electrodes on the scalp surface in accordance with standardized electrode placement systems. It measures the sum of post-synaptic potentials generated predominantly by pyramidal neurons in the cerebral cortex, providing a high temporal resolution index of neural activity in real time (Niedermeyer & Lopes da Silva, 2005; Buzsáki et al., 2012). EEG is characterized by its sensitivity to brain oscillations that reflect different cognitive states and levels of arousal, making it an extremely useful tool for the study of executive functions, attention, working memory, and perception, even in applied contexts such as sport psychology and neurological rehabilitation (Makeig et al., 2004; Thompson et al., 2008). EEG is able to provide information with high temporal resolution (on the order of milliseconds), making it particularly useful for studying the temporal dynamics of brain activity (Luck, 2014). However, its spatial resolution is relatively low, due to the volume conduction effect that reduces the accuracy in localizing the underlying neural sources (Nunez & Srinivasan, 2006).

5.1. Nature of the EEG signal

EEG detects and records the brain’s electrical activity generated by the postsynaptic potentials of cortical neuronal populations, primarily the pyramidal neurons located in the cerebral cortex, which constitute the main excitatory cell type of the cortex (Niedermeyer & Lopes da Silva, 2005; Buzsáki et al., 2012). These neurons, oriented perpendicularly to the cortical surface, generate electric fields when subjected to changes in membrane potential following synaptic transmission. The electrical activity detected by EEG is not the result of individual action potentials—whose duration and propagation are too rapid and localized to be detected at the surface level—but rather derives from slow postsynaptic potentials (EPSPs and IPSPs), whose spatial and temporal summation gives rise to measurable extracellular currents (Murakami & Okada, 2006). These potentials are produced by ionic flows through the cell membrane following the opening of ion channels stimulated by neurotransmitters. The resulting transmembrane ionic balance generates a temporary electrical dipole, with a “negative pole” where cations enter (typically at the apical dendrites) and a “positive pole” where they exit (usually at the soma or basal dendrites). This produces an intracellular current (within the membrane) and a return extracellular current. If a sufficient number of neurons is activated synchronously and coherently—that is, with the same orientation—their dipoles sum (spatial summation), producing an electric field (Nunez & Srinivasan, 2006).

Once generated at the intracortical level, EEG signals propagate through several layers of biological tissue: first through the cerebral gray and white matter, then through the cerebrospinal fluid, followed by the meninges and cranial bones, and finally through the scalp. During this propagation, the signals undergo significant attenuation and distortion due to the different conductive and resistive properties of the tissues they traverse, which is why the spatial resolution of EEG is limited compared to other neuroimaging techniques (Michel & Brunet, 2019; Olejarczyk & Sobieszek, 2021).

The recorded EEG signal is an extracranial projection of cortical dipole activity:

- A positive potential (positive pole) on the scalp surface generally corresponds to a current directed toward the depths of the brain.
- A negative potential (negative pole) on the surface corresponds to a current directed toward the cortical surface.

EEG does not directly measure dipoles but rather the potential differences between two or more electrodes placed on the head. These differences reflect the temporal variations of the underlying cortical dipole activity (Jackson & Bolger, 2014).

5.2. Electrode Placement Systems

Electrode placement systems, developed and internationally adopted, are based on anatomical and geometric principles that allow for a homogeneous and representative distribution of electrodes across the scalp surface, corresponding to the underlying brain morphology.

The most widely used configuration is the international 10–20 system, originally proposed by Jasper in 1958. The name refers to the relative distances between electrodes, which are either 10% or 20% of the total length of specific cranial segments measured between anatomical landmarks (nasion, inion, preauricular points). In this system, the scalp is divided according to a spatial grid, where each point is identified by an alphanumeric code that combines:

- A letter indicating the underlying brain region (Fp=frontopolar, F=frontal, C=central, P=parietal, O=occipital, T=temporal),
- An even number (right hemisphere), an odd number (left hemisphere), or a "Z" indicating positions on the midline (zero line).

The 10–20 system includes a minimum of 21 electrodes but can be extended to high-density configurations (American Clinical Neurophysiology Society, 2006; Seeck et al., 2017).

This system allows for consistent and replicable electrode positioning across individuals and institutions, making it suitable for both clinical and research purposes. Its structured and standardized layout supports comparability across studies, longitudinal recordings, and integration with neuroimaging data (Jurcak, Tsuzuki, & Dan, 2007).

To improve spatial resolution and support advanced applications such as cortical source localization and functional brain mapping, high-density electrode systems have been developed:

- 10–10 System: This system extends the standard 10–20 montage by adding intermediate electrodes spaced at 10% intervals of the total inter-electrode distance. It typically includes 64 or more electrodes and is particularly useful for neurocognitive studies, advanced clinical applications, and experimental research (Seeck et al., 2017).
- 10–5 System: This is a further densification of the 10–10 system, with electrodes placed every 5% of the inter-electrode distance, leading to arrays of 128, 256, or more channels. This approach

is used in cutting-edge neuroscience research and detailed cortical source modeling (Luu & Ferree, 2005).

Electrode positioning is performed either manually with a flexible measuring tape or using computerized 3D coordinate systems (digitizers), which allow for co-registration with structural MRI images, ensuring high spatial accuracy (Koessler et al., 2009). Electrode mounting may be carried out using preconfigured elastic caps, EEG headgear, or individually mounted electrodes with conductive paste and adhesive, depending on the type of study, the recording duration, and subject sensitivity.

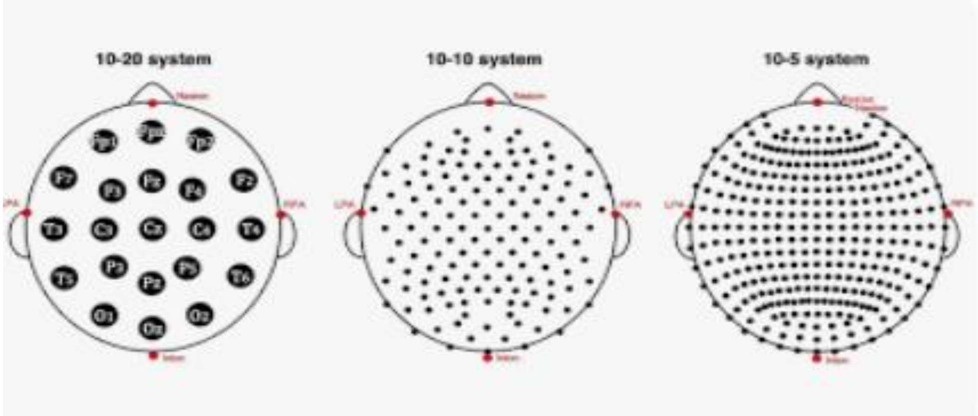


Fig 1: Comparison between the three montage systems.

The choice of montage system depends on several factors:

• Study objective: Routine clinical evaluations typically use the 10–20 system, while research on complex cognitive functions or source localization benefits from high-density systems (Michel & Murray, 2012).

• Target population: In children or neurologically vulnerable patients, a compromise between electrode density and subject comfort is often necessary.

• Available equipment: Modern high-density EEG interfaces require compatible software and hardware for multi-channel management, calibration, and signal processing (Babiloni et al., 2020).

The use of standardized electrode placement systems enables the acquisition of high-quality signals, inter-study comparability, reproducibility of results, and integration with other neurophysiological and neuroimaging data. The evolution toward increasingly dense and precise systems reflects the current trend toward quantitative, high-resolution spatial neurophysiology that is more deeply integrated into both research and clinical practice (Michel & Brunet, 2019).

5.2.1 Applications

In the sports domain, the use of EEG has gained increasing relevance for investigating the brain dynamics underlying motor and cognitive performance. In particular, oscillations in the theta, alpha, beta, and gamma bands have been associated with different cognitive processes involved in attentional regulation, error monitoring, motor planning, and rapid decision-making. For example, an increase in frontal theta band power has been correlated with heightened attentional demand and the engagement of executive functions during high-complexity tasks (Cavanagh & Frank, 2014; Mitchell et al., 2008), whereas a desynchronization in the parietal alpha band is frequently interpreted as an index of cortical activation and visuo-spatial processing (Pfurtscheller & Lopes da Silva, 1999; Klimesch, 2012).

For example, EEG has been increasingly employed to investigate the neural dynamics underlying optic flow perception, beyond time-locked event-related potentials. Oscillatory EEG activity, particularly in the alpha and beta frequency bands, has been shown to modulate during the processing of visual motion consistent with optic flow, reflecting sensorimotor integration and attentional engagement (Keshava et al., 2020; Chuang et al., 2018). For instance, decreases in parietal alpha power have been associated with increased visual attention to motion cues that signal self-motion through the environment (Benjamin et al., 2018). Furthermore, studies using Mobile Brain/Body Imaging (MoBI) setups have demonstrated that optic flow during real or virtual locomotion elicits widespread EEG changes in both sensorimotor and vestibular-related cortical areas, supporting the role of EEG in studying active perception during movement (Gramann et al., 2014; Gwin et al., 2010).

EEG has emerged as a powerful tool for investigating the temporal dynamics of multisensory integration beyond time-locked event-related potentials (ERPs), allowing for the study of oscillatory activity and functional connectivity between brain regions. Studies have shown that multisensory integration is associated with changes in oscillatory power, particularly in the theta, alpha, and gamma bands, which reflect processes such as sensory binding, attentional modulation, and cross-modal prediction (Keil & Senkowski, 2018; Doesburg et al., 2008). For example, enhanced gamma-band synchronization between sensory cortices has been linked to successful audiovisual integration, supporting the notion that phase coupling facilitates inter-regional communication during multisensory processing (Senkowski et al., 2008). Similarly, reductions in alpha power have been observed during congruent multisensory stimulation, suggesting a release of inhibition in sensory-specific areas to facilitate integration (Van Driel et al., 2014). EEG connectivity analyses, such as coherence and phase-locking value (PLV), have also been used to reveal dynamic communication between modality-specific and associative cortical areas during cross-modal tasks (Hipp et al., 2011). Importantly, mobile EEG and naturalistic paradigms now enable the study of multisensory integration during active behavior, such as walking or interacting with real-world stimuli, expanding our understanding of how the brain integrates sensory inputs in ecologically valid contexts (Debener et al., 2012; Jungnickel & Gramann, 2016).

5.2.2. EEG Frequency Bands

EEG detects electrical oscillations that manifest as sinusoidal waves characterized by specific quantitative and qualitative parameters:

• Amplitude, measured in microvolts (μV), which reflects the intensity of the electrical activity;
• Frequency, expressed in Hertz (Hz), representing the number of cycles per second;
• Morphology, referring to the shape of the wave;

• Spatial distribution, referring to the topographic localization of the signal over the cortical area (Niedermeyer & Lopes da Silva, 2005).

EEG specifically records oscillations of brain electrical activity manifesting as sinusoidal waves with distinct parameters: amplitude (microvolts), frequency (Hertz), morphology, and spatial distribution. These signals reflect the functional state of the central nervous system and vary according to physiological conditions (wakefulness, sleep, attention) or pathological states (epilepsy, encephalopathies, brain lesions) (Buzsáki, 2006).

The main frequency bands recognized in the neurophysiological literature are: delta, theta, alpha, beta, and gamma. Each has specific features in terms of frequency range, amplitude, predominant topographical localization, and neurocognitive implications (**Fig.** 1).

- Delta Band (0.5–4 Hz):

  Delta is the lowest frequency and highest amplitude band in the human EEG. It is particularly prominent during deep non-REM sleep (stage N3), where it is associated with physiological recovery processes and memory consolidation. Delta wave generation is typically attributed to thalamo-cortical synchronization mechanisms and reflects states of low cortical activation (Achermann & Borbély, 1997). In wakefulness, excessive delta activity in cortical regions may indicate focal or diffuse brain pathology, such as structural lesions, encephalopathies, or metabolic dysfunctions. In clinical practice, localized delta activity during wakefulness is an important marker of cortical alterations (Nunez & Srinivasan, 2006).

- Theta Band (4–8 Hz):

  Theta activity is commonly observed during drowsiness, transition to sleep (stage N1), and in deep relaxation or meditation. It is particularly abundant in children, while in adults it appears transiently during relaxed wakefulness. From a cognitive perspective, theta waves are associated with memory encoding and retrieval, spatial navigation, and emotional regulation (Klimesch, 1999; Mitchell et al., 2008). In awake adults, elevated theta in fronto-central regions may be linked to cognitively demanding tasks requiring executive control, error monitoring, and response inhibition. Increased theta activity is often observed in neuropsychiatric disorders such as ADHD and depressive disorders (Barry et al., 2003).

- Alpha Band (8–13 Hz):

Alpha waves are among the most studied and characteristic EEG rhythms. They are most evident in occipital and parietal regions during relaxed wakefulness with closed eyes and tend to decrease with eye opening or cognitive activation. Alpha activity is generally interpreted as an indicator of functional inactivity or cortical inhibition. According to the "alpha inhibition hypothesis," its presence reflects an active suppression mechanism of task-irrelevant cortical areas (Jensen & Mazaheri, 2010). It has also been linked to information processing efficiency and visuospatial attention modulation. Distinct subbands of alpha, such as lower alpha (8–10 Hz) and upper alpha (10–13 Hz), seem to be involved in different cognitive functions, related to general relaxation and attentive vigilance respectively (Klimesch, 1999).

- Beta Band (13–30 Hz):

  Beta activity is associated with focused attention, alertness, active mental engagement, and motor planning. Beta waves are frequently recorded in frontal and central regions and become particularly prominent during movement or motor preparation, reflecting activation of motor and premotor circuits (Pfurtscheller & Lopes da Silva, 1999). Beta oscillations are also involved in modulating cortical motor inhibition and top-down cognitive control. Excessive beta activity can be observed in anxiety or hyperarousal, whereas marked reduction is noted in neurodegenerative disorders such as Parkinson's disease. Beta rhythms show strong resonance with basal ganglia and thalamo-cortical system activity (Engel & Fries, 2010).

- Gamma Band (>30 Hz, typically 30–100 Hz):

  Gamma is the highest frequency EEG band typically analyzed. It has been associated with higher-order cognitive processes such as multisensory integration, perceptual consciousness, selective attention, working memory, and the "binding" of information (Singer, 1999; Jensen et al., 2007). Gamma oscillations reflect short-term synchronization between distinct neuronal populations and are thought to play a key role in functional communication between cortical and subcortical areas. However, due to their low amplitude and susceptibility to muscle artifacts (EMG), recording and interpreting gamma activity requires refined filtering and analysis techniques. Aberrant gamma activity has been reported in neurological and psychiatric disorders such as schizophrenia, bipolar disorder, and epilepsy (Uhlhaas & Singer, 2010).

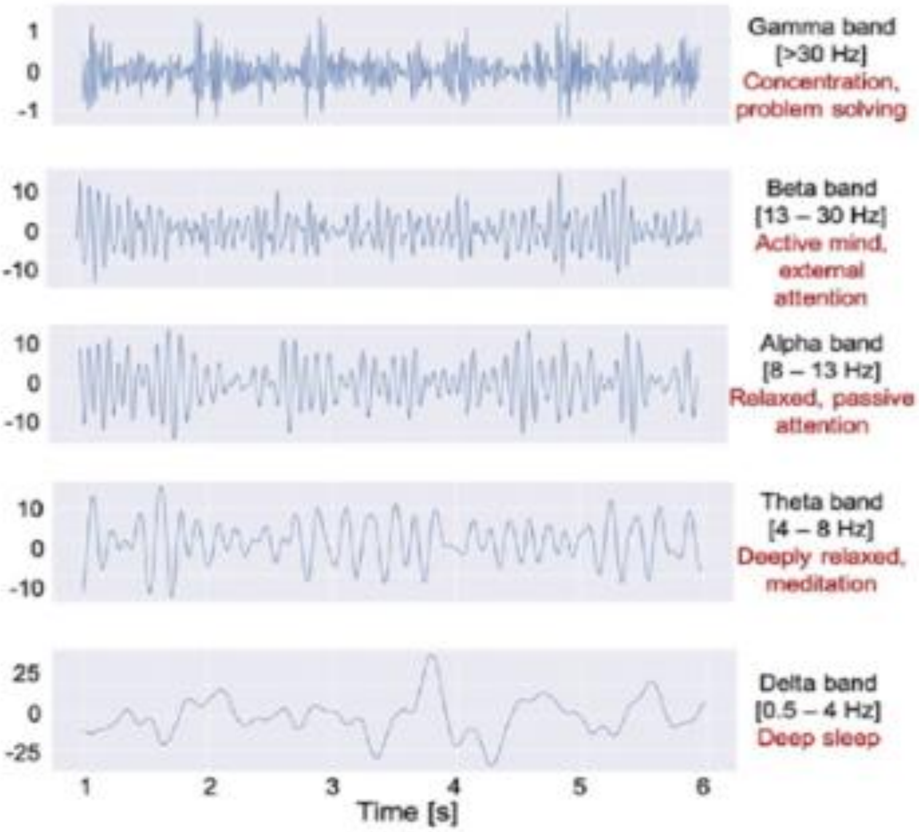


Fig 1: Representation of the main brainwave frequency bands recorded through electroencephalography (EEG).

5.3. Event-Related Potentials (ERP)

One of the most relevant applications of electroencephalography (EEG) is the study of *Event-Related Potentials* (ERP), which are electrophysiological responses manifesting as changes in cerebral electrical potential, time-locked to the presentation of a sensory, motor, or cognitive stimulus. ERPs provide a direct measure of neural processing in response to specific events and are a crucial tool for investigating the temporal dynamics of perception, attention, memory, and other cognitive processes.

From a technical standpoint, ERPs are obtained by averaging multiple EEG epochs that are temporally aligned to the event of interest. This averaging process is essential to improve the signal-to-noise ratio (SNR), allowing the isolation of stimulus-related components from the background EEG activity, which appears as random noise. Since evoked brain responses tend to occur consistently in relation to the stimulus, whereas spontaneous activity is not phase-locked, averaging suppresses the noise and enhances the coherent signal.

ERPs appear as sequences of positive and negative deflections relative to a baseline, each characterized by latency, polarity, amplitude, and scalp topography. Components are usually named based on their polarity—positive (P) or negative (N)—and their average latency in milliseconds after the stimulus onset. Post-stimulus components are associated with specific neurophysiological or cognitive processes, such as:

- Early components (within 20–200 ms): reflect initial sensory processing (visual, auditory, somatosensory).
- Intermediate components (200–400 ms): associated with selective attention, discrimination, and stimulus relevance.
- Late components (>400 ms): involved in higher-order cognitive functions such as evaluation, working memory, and decision-making.

The spatial topography of ERP components, observed through their voltage distribution across EEG electrodes, also allows inferences about the probable cortical sources, although with limited spatial resolution compared to other imaging techniques.

5.3.1. Movement-Related ERPs

ERP components associated with movement reflect electrocortical activity involved in the processes of preparation, planning, and execution of voluntary movement and constitute an important tool for studying motor cortical dynamics. Among these, one of the most studied is the Bereitschaftspotential (BP), also known as the readiness potential (RP). In more recent literature, this activity is commonly referred to as the movement-related potential (MRP) or, more precisely, the movement-related cortical potential (MRCP). The first component of the MRCP, observable for simple movements, emerges over fronto-central regions and indicates a progressive increase in cortical excitability preceding the initiation of the motor command (Shibasaki & Hallett, 2006).

Immediately preceding the onset of the motor act, the motor potential (MP) is observed, a negative deflection associated with the transmission of the actual signal for muscular activation. This is sometimes followed by the negative slope (NS'), a rapid intensification of cortical negativity, considered an expression of the finalization of motor preparation.

After execution, a post-movement positivity (PMP) can be observed, which is interpreted as a reflection of processes related to movement monitoring and proprioceptive and efferent feedback (Shibasaki & Hallett, 2006).

More recent studies have suggested a critical reflection on the functional interpretation of the BP: for example, Schmidt et al. (2016) hypothesized that the BP does not necessarily represent a causal factor for movement, but rather a neural correlate of voluntary intention, indicating a predisposition to act but not inevitably determining its initiation. This perspective challenges the deterministic conception of the BP as an automatic trigger of movement and suggests a greater complexity in the relationship between preparatory activity and motor decision.

With the advent of mobile electroencephalography (Mobile Brain/Body Imaging, MoBI), it has become possible to record MRCPs even during dynamic and natural movements, such as walking. These studies have confirmed that the temporal pattern of motor ERP components is preserved during locomotion, although with variations in amplitude and topography related to the biomechanical and sensory complexity of the movement (Makeig et al., 2009; Gramann et al., 2010). This has opened new perspectives for the neurophysiological analysis of motor control in ecologically valid contexts, making MRCPs an essential tool for understanding the brain mechanisms underlying voluntary locomotion and self-initiated movement.

In more complex cognitive tasks, late components such as the Late Positive Component (LPC) or Late Positive Potential (LPP) are observed. These reflect evaluative, affective, or mnemonic processing of stimuli. The LPP is modulated by the emotional characteristics of stimuli and typically shows a centro-parietal distribution (Hajcak et al., 2010).

Overall, the analysis of stimulus-locked ERP components allows a fine-grained, non-invasive decomposition of the temporal dynamics of cognitive processing, making ERPs particularly valuable in both clinical and experimental contexts for exploring perceptual, attentional, and decisional functions.

5.3.2. Stimulus-related ERP Components

Stimulus-locked ERP components represent the temporal and spatial manifestations of electrocortical activity related to the processing of relevant sensory events. These components are extracted by averaging EEG responses time-locked to the onset of a stimulus (visual, auditory, somatosensory, etc.) and reflect successive stages of neural processing, from early perception to semantic and decisional evaluation (Luck, 2014).

Among the earliest components are the P1 and N1, which emerge within the first 100–200 ms after stimulus presentation and are considered markers of early sensory processing. The P1, a positive deflection maximal over occipital regions between 80–130 ms, is sensitive to physical characteristics of the stimulus and is modulated by spatial attention (Hillyard et al., 1998). The N1, a negative deflection occurring around 100–180 ms post-stimulus, is typically observed over centro-parietal regions for auditory stimuli and occipito-temporal areas for visual stimuli, reflecting selective and discriminative processing (Näätänen & Picton, 1987).

P1 is an early sensory-attentional positive component that appears approximately 80–130 ms after the presentation of a visual stimulus and represents initial visual processing (bottom-up) (Luck & Hillyard, 1994). It is typically recorded over occipital and posterior parietal electrodes (especially O1, O2, PO7, PO8) and reflects activity in the early stages of the visual pathway (V1/V2/V3), particularly in the occipito-temporal cortex (Clark & Hillyard, 1996). Specifically, it is primarily generated in the extrastriate visual cortex, in areas V2/V3, cuneus, lingual gyrus, and posterior visuospatial-attentive areas (Di Russo et al., 2003). ERP–fMRI and MEG studies also indicate the involvement of the fusiform gyrus and the posterior parietal lobe, especially when visual attention is manipulated (Heinze et al., 1994; Mangun, 1995). It is sensitive to the retinotopic position of the stimulus and to the direction of visual attention, and its amplitude increases when attention is voluntarily directed toward the position of the stimulus, while it decreases under distraction, cognitive load, or unexpected stimulus location (Luck et al., 2000; Mangun & Hillyard, 1991). In visuomotor tasks, P1 is crucial for the early selection of the relevant visual stimulus that guides motor action and reflects the prioritization of the target stimulus in visual space, facilitating the visuomotor transformation (Praamstra et al., 2006). It functions as a sensory filter, as indicated by the fact that it is modulated by expectation and stimulus relevance (Hillyard & Anllo-Vento, 1998). During walking, it plays a role in early visual processing of environmental signals relevant for stepping (e.g., obstacles, terrain variations, movement direction), and is modulated by spatial visual attention while walking, especially when gait is visually guided or requires rapid adjustments (Nordin et al., 2020). In complex conditions (e.g., dual task, walking on an unstable path), P1 amplitude may increase as an indicator of visuo-attentive compensation (De Sanctis et al., 2014). It shows a direct proportional association with BP and pN (Brunia & van Boxtel, 2001; Bekker et al., 2005), since motor preparation and anticipatory attention increase sensitivity to stimulus features relevant to the task, thereby enhancing the already prepared action. Regarding post-stimulus components, P1 is part of a hierarchical process that also includes N1 and P2; this process begins with sensory orientation and early visual processing represented by P1, continues with conscious visual attention (N1), and ends with decision preparation, represented by P2 (Luck & Kappenman, 2012).

N1 is a negative wave that appears approximately 100–180 ms after stimulus presentation, with latency slightly varying depending on the modality (visual, auditory, somatosensory) (Näätänen & Picton, 1987; Luck & Hillyard, 1994). It is most evident in posterior occipito-parietal channels in visual tasks (e.g., PO7, PO8) and in central-frontal channels in auditory tasks (Vogel & Luck, 2000). It can be divided into two subcomponents: anterior N1, related to attentional orienting, and posterior N1, related to stimulus discrimination (Hillyard & Anllo-Vento, 1998; Hillyard et al., 1998). It is involved in stimulus classification and discriminative processing preparatory to the decision-making process (Eimer, 1996). N1 is sensitive to the spatial position and behavioral relevance of the stimulus, with clear top-down modulation; in fact, it is influenced by attention, expectation, instructions, or task context (Luck et al., 2000; Mangun, 1995). ERP–fMRI and dipole source studies indicate that visual N1 is generated in the occipito-temporal extrastriate cortex (V3/V4), posterior parietal lobe (for the spatial component), and dorsal frontal cortex (in attentional contexts) (Di Russo et al., 2002; Foxe et al., 2008).

In visuomotor tasks, N1 reflects an important phase of selective processing of the visual stimulus, fundamental for rapidly identifying the relevant characteristics of an object or visual scene that will guide the motor response (Luck & Hillyard, 1994). It is also associated with sensory filtering, which allows irrelevant stimuli to be excluded and attention to be directed toward the visual target to be reached or manipulated (Vogel & Luck, 2000); with visuo-spatial integration, essential for calculating the position of the object and programming a precise motor action (Praamstra et al., 2006); and with action preparation, since it modulates the effectiveness of visuomotor transformation and motor response timing (Eimer, 1996). During locomotion, N1 is important for visual sensory monitoring, helping to timely identify obstacles or terrain variations (Nordin et al., 2020). It is involved in the allocation of visual attention in space, particularly in situations where walking requires rapid adaptation or posture control on unstable surfaces (De Sanctis et al., 2014). N1 modulation during walking is linked to the need to integrate visual signals with vestibular and proprioceptive ones to maintain balance and spatial coordination (Woollacott & Shumway-Cook, 2002). In dual-task conditions (e.g., walking while performing a cognitive task), N1 amplitude may vary as an indicator of attentional resources allocated between walking and the cognitive task (Patel et al., 2014). It is associated with BP, pN, P1, N2 (involved in more advanced cognitive processing, such as cognitive control, complex discrimination, and stimulus relevance; Folstein & Van Petten, 2008), and P2 (associated with processing of relevant stimuli and decision response preparation, working in synergy with N1 to integrate sensory and cognitive information; Crowley & Colrain, 2004).

The P2 component, a positive deflection occurring around 150–250 ms, is involved in perceptual categorization and the detection of salient or novel stimuli (Potts et al., 1996). It is influenced by both physical stimulus features and cognitive variables such as expectations and learning.

A key component in cognitive ERP research is the N2, a negativity occurring between 200 and 350 ms post-stimulus, often observed in go/no-go or oddball tasks. The N2 is associated with cognitive conflict, inhibitory control, and monitoring of discrepancies between the stimulus and the subject’s expectations (Folstein & Van Petten, 2008). In visual tasks, the N2pc (posterior-contralateral N2), recorded over occipito-parietal sites contralateral to the target stimulus, reflects visuospatial selective attention (Luck & Hillyard, 1994).

One of the most widely studied ERP components is the P3 (or P300), which occurs between 300–600 ms post-stimulus. The P3 is a positive ERP component occurring after significant or unexpected stimuli, typically maximal at parietal sites (Pz), though its scalp distribution varies by subtype and task (Polich, 2007). It is divided into P3a, an earlier fronto-central wave (250–280 ms) linked to automatic attention and orienting toward novel stimuli, and P3b, a later parietal wave (300–500 ms) reflecting working memory updating and conscious processing of task-relevant events (Polich, 2007).
Functionally, the P3 supports attentional allocation, working memory updating, stimulus evaluation, decision-making, and motor preparation (Kok, 2001; Polich, 2007). Source localization and ERP–fMRI studies show that P3b is mainly generated in the posterior parietal cortex, while P3a involves the medial and dorsolateral prefrontal cortex, along with the thalamus and limbic system, which modulate motivation and attentional integration (Linden, 2005; Polich, 2007).

In visuomotor and walking tasks, P3 indexes the integration of visual and motor signals, enabling memory updating and action planning (Polich, 2007; Kok, 2001). During walking, it supports environmental monitoring and motor control adaptation, sustaining coordination under complex or changing conditions (Verleger, 1997; Sipp et al., 2013). In multitasking, larger P3 amplitudes indicate cognitive compensation through enhanced attentional and executive control (De Sanctis et al., 2014).

Conceptually, P3 represents the culmination of a processing hierarchy: from sensory orienting (P1), through discrimination (N1, P2), to resource allocation and memory updating (P3) (Polich, 2007). Its amplitude is modulated by pre-stimulus activity (pN, BP), where stronger anticipatory preparation produces faster and larger P3 responses (Brunia & van Boxtel, 2001), and by early sensory processing quality (N1, P2), which enhances memory updating efficiency (Luck, 2014; Polich, 2007).

5.3.3. ERP and Multisensory Integration

Numerous studies have shown that multisensory integration specifically modulates the amplitude and latency of early ERP components, suggesting the existence of automatic and pre-attentive mechanisms of sensory fusion (Fort, Delpuech, Pernier, & Giard, 2002). In particular, the N1 component has been frequently associated with processes of spatio-temporal alignment between visual and auditory signals. An enhancement of the N1 in congruent multisensory conditions (e.g., a sound and a flash originating from the same location) suggests early facilitation of sensory processing due to integration (Molholm, Ritter, Murray, Javitt, Schroeder, & Foxe, 2002).

Subsequent ERP components, such as the P2 and P3, reflect more advanced stages of multisensory processing, often related to attention allocation, stimulus discrimination, and decision-making responses. The modulation of the P3 in multisensory tasks has been interpreted as an index of the efficiency of perceptual decision-making mechanisms in the presence of congruent or incongruent sensory information (Talsma, Mulckhuyse, Slagter, & Theeuwes, 2007). In the sports domain, these components can be used to assess the speed and accuracy of multisensory processing in situations that require a rapid and contextually appropriate response, such as the reaction to audiovisual cues during gameplay (Williams, Davids, & Williams, 1999).

The use of ERPs in the study of multisensory integration presents numerous advantages, including the ability to distinguish between bottom-up and top-down processes, identify the sequential stages of integration, and objectively compare individuals with different levels of motor or cognitive expertise (Foxe & Schroeder, 2005). In sporting contexts, ERP has proven to be a sensitive tool for detecting differences in the timing of multisensory processing between expert and novice athletes, revealing more efficient and anticipatory processing in the former (Di Russo, Pitzalis, Aprile, & Spinelli, 2005).

Moreover, ERP paradigms have been employed to study the plasticity of multisensory integration following specific training programs. For example, protocols including combined visuoauditory or visuo-proprioceptive exercises have shown significant effects in modulating ERP responses, suggesting neural adaptation toward more effective sensory integration (Shams & Seitz, 2008). These results have important implications for the optimization of sports performance, the design of rehabilitative interventions, and the monitoring of recovery after injury (Hötting & Röder, 2004).

Finally, ERP represents a useful index for evaluating potential alterations in integrative processes under pathological or post-traumatic conditions. In athletes with a history of concussion, for instance, a delay in ERP components associated with multisensory integration has been observed, indicating a potential deficit in the neurocognitive mechanisms involved in sensory information fusion (Guskiewicz, Riemann, Perrin, & Nashner, 2001; Broglio, Pontifex, O'Connor, & Hillman, 2009). Such alterations may persist even in the absence of overt clinical symptoms, underscoring the importance of ERP as a diagnostic tool complementary to behavioral tests.

5.3.4. ERP and Optic Flow

Among the numerous multisensory stimuli that the brain must integrate to effectively guide behavior, optic flow represents a fundamental visual component for the perception of egocentric movement and spatial orientation.

The use of ERP in the study of optic flow makes it possible to identify the temporal stages in which visuomotor information is processed by the brain, highlighting the neural dynamics that support the perception of self-motion and action planning. Early ERP components, such as the N2, have been associated with the automatic analysis of coherently moving visual stimuli, suggesting a preattentive processing of optic flow in the extrastriate visual cortex (Heinrich, Mell, & Bach, 2009; Hoffmann et al., 2001). In particular, studies using visual oddball paradigms have shown that the presentation of deviant optic flow patterns (e.g., changes in direction or motion coherence) evokes characteristic ERP responses, such as visual mismatch negativity (vMMN) and an enhanced N2, indicating automatic detection of deviation from the standard stimulus (Pavlova et al., 2002; Kremláček et al., 2004). These results support the hypothesis that optic flow processing is sustained by predictive and automatic mechanisms, sensitive to sub-perceptual variations in visual motion.

The P3 component, generally associated with decision-making processes and voluntary attention, has also been observed in response to significant changes in optic flow patterns, especially in tasks requiring active detection or discrimination of motion direction (Mishra, Martinez, Sejnowski, & Hillyard, 2007). The amplitude and latency of the P3 have been shown to be modulated by the degree of optic flow coherence, suggesting that the quality and predictability of visual input influence higher-order processing stages (Kaiser, Strüber, & Herrmann, 2004).

ERPs have also been used to characterize the spatio-temporal profile of the effect of optic flow direction coherence on visual evoked potentials (VEP), while at the same time localizing their sources (Pitzalis et al., 2013). By combining VEP and fMRI analyses, it was observed that motion processing begins in V1 with the C1 component, about 50 ms after stimulus onset. This component peaks at 75 ms and is followed by the P1 in ventral extrastriate areas (V3A), probably the LOR region, as well as by the P130 and the N140, localized respectively in MT+ and V6. Finally, the N180 arises in V3A and the P230 in V6. It was found that coherence enhances the positive components P130 and P230, and the N140, indicating more efficient visual and attentional processing. In contrast, incoherence enhances the N180, reflecting a greater perceptual load and less efficiency. This study helped confirm the preference of V6 and MT+ for coherent motion, and of V3A for the random one.

Finally, recent studies have explored the effects of training and repeated exposure to optic flow stimuli on ERP activity, showing significant neural plasticity in terms of anticipation and motion discrimination (Miller, Sutterer, & Boehler, 2015). These findings suggest the potential use of ERP paradigms to monitor perceptual adaptation in visuomotor training programs or in rehabilitation protocols for balance and spatial navigation disorders.

In summary, the integration of event-related potentials in the study of optic flow allows for a precise investigation of the temporal and functional dynamics of visual motion processing, providing important insights into the neural processes involved in spatial perception, active navigation, and motor control. The ability to correctly integrate the visuospatial information provided by optic flow becomes crucial when locomotion is accompanied by additional cognitive demands, as in dual-task paradigms.

5.3.6. Pre-stimulus components

Regarding the pre-stimulus phase, the three slow negativities are present before the stimulus onset in visual tasks. The Bereitschaftspotential (BP), the prefrontal Negativity (pN), and the visual Negativity (vN),

The BP begins 1–3 seconds before the onset of the stimulus and reaches its peak at the onset of the stimulus. As stated above for the MRCP, the BP is associated with motor preparation, motor prediction (e.g., Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018), and the cognitive preparation of voluntary movement (e.g., Gentsch et al., 2016; Ody et al., 2023; Reznik et al., 2018), and is generated in the supplementary motor area (SMA) (e.g., Di Russo et al., 2017; Shibasaki & Hallett, 2006) and is also observed in ipsilateral and contralateral premotor areas (Kristeva et al., 1991; Cunnington et al., 2005) and in the primary motor cortex (M1) (Luft & Bhattacharya). The BP is described as having a biphasic trend: in this context, an early BP is distinguished, linked to the general and nonspecific intention to move (e.g., Schurger et al., 2021; Shibasaki, 2012), and a late BP, related to the preparation of the specific movement (e.g., Shibasaki & Hallett, 2006) and correlated with performance (e.g., Deecke, 2012; Dennet 2005; Mele et al., 2007), as it indicates top-down attentional control (e.g., Di Russo et al., 2019), which allows real-time adaptation to environmental demands (e.g., Kornhuber & Deecke, 2016; Di Russo et al., 2019). In fast cognitive tasks, a relationship has been demonstrated between the amplitude of the late BP and reaction time (RT) (e.g., Di Russo et al., 2019). In complex movements such as reaching, grasping, or pantomimes, the BP is located more posteriorly (Bozzacchi et al., 2012; Wheaton et al., 2005a; Wheaton et al., 2005b), in the posterior parietal cortex (PPC), and seems to be associated with goal-directed movement, towards a target. In this case, it is referred to as posterior BP (pBP). In visuomotor tasks, BP is involved in the voluntary preparation of visually guided movement (Schlüter et al., 2001), while pBP is responsible for visuomotor transformation (translating visual coordinates into motor coordinates), monitoring of spatial position of the body and objects, and prediction of motor outcome (Sarrias-Arrabal et al., 2022). Consequently, during locomotion, the former reflects preparation for the initiation of locomotion, in the initial phase of the step (Velu & de Sa, 2013), while the latter is involved in the spatial-motor coordination of steps, thus in the integration of visual, vestibular, and proprioceptive signals to adapt the step (Almeda & Leibel, 2013; Tarkka, 2017).

The prefrontal negativity (pN) is an anticipatory event-related potential, typically observed in prefrontal regions developing around −800 to −600 ms and progressively increases in amplitude, reaching its maximum immediately before the stimulus (Berchicci et al., 2012; Di Russo et al., 2013; Bianco et al., 2020). It manifests as a negative deflection preceding stimulus onset, especially in visuomotor discriminative tasks without external cues, where both temporal preparation and event-related preparation (anticipation of the category or nature of the upcoming stimulus) are required (Bianco et al., 2020; Berchicci et al., 2020). The pN thus represents a neurophysiological index of proactive control, reflecting the ability of the cognitive system to set up processing mechanisms in anticipation of an optimal response. This component is associated with sustained prefrontal activity preceding the decision phase and supporting proactive control mechanisms (Berchicci et al., 2015; Bianco et al., 2022). In particular, it seem to play a central role in anticipatory inhibition, supporting the suppression of inappropriate motor and cognitive responses.

Several studies have shown that the amplitude of the pN is positively correlated with behavioral accuracy: larger pN amplitudes are associated with a higher number of correct responses and with fewer errors, both in go/no-go tasks and in tasks requiring high attentional load (Di Russo et al., 2019; Bianco et al., 2020). This relationship highlights the role of the pN as an anticipatory “cognitive brake”, a form of top-down control aimed at maximizing accuracy at the expense of speed, thus contributing to the trade-off between speed and accuracy (Berchicci et al., 2020).

Finally, more recent studies using Temporal Spectral Evolution (TSE) have demonstrated that the pN is primarily sustained by activity in the sub-delta band, highlighting the role of slow oscillatory dynamics in anticipatory cognitive preparation (Berchicci et al., 2015; Bianco et al., 2022). This spectral pattern suggests that the pN constitutes a fundamental neurophysiological mechanism for optimizing the interplay between attentional processes, movement planning, and behavioral accuracy.

The BP and the pN, in the context of perceptual-discriminative tasks, can be considered as part of a brake/accelerator system in which the BP acts as a propeller for action, for movement. At the same time, the pN intervenes, based on an evaluation of environmental contingencies, to block unnecessary or no longer necessary movement. More specifically, the decision whether to provide or withhold a response is made based on a continuous accumulation of information, of evidence, until a certain threshold is reached (Ratcliff, 1978). Since this information gathering takes time, in tasks where the decision must be made very quickly, the probability of error is much higher (Wenzlaff et al., 2011). Consequently, it is necessary to reach a compromise between the time limits within which the response must be given and the amount of information accumulated, which is directly correlated with response accuracy. This phenomenon is called the response accuracy/speed trade-off (SAT) (Bogacz et al., 2006) and is modulated by internal predictive models (Di Russo, 2019; Perri et al., 2014) that regulate proactive behavior (e.g., Aron, 2011).

The visual negativity (vN) is a slow pre-stimulus ERP deflection maximal over parieto-occipital scalp sites—often contralateral to the expected hemifield—originating from occipital–extrastriate generators and indexing modality-specific sensory readiness that biases early visual processing prior to target onset (Di Russo et al., 2019; Bianco et al., 2019). In tasks that require discrimination, inhibition, or speeded visuomotor decisions, vN emerges several hundred milliseconds before stimulus appearance and scales with attentional orienting and expectation in visual cortex (e.g. Bianco et al., 2019; Di Russo et al., 2019). Critically, vN amplitude predicts sensory gain and performance benefits by "priming" post-stimulus occipital responses: when upcoming events are visual or audiovisually congruent, vN enlarges and starts earlier, and this anticipatory bias increases the magnitude of early sensory evoked components (visual P1), tightening visuomotor latencies (Fiorini et al., 2021; Fiorini et al., 2023). Evidence that vN is a anticipatory visual process—not merely predictability-driven carryover—comes from designs manipulating sensory modality and predictability: vN is larger for visual than auditory foreperiods, is enhanced by multisensory (AV) expectancy beyond the arithmetic sum of unimodal responses, and retains modality-specific topography under temporal cueing and sustained/transient attention, consistent with an upstream visual bias that preconditions early sensory coding for impending action (Bianco et al., 2019; Fiorini et al., 2021; Di Russo et al., 2020; Fiorini et al., 2023). Finally, during movement per se, anticipatory brain states adapt: recent work targeting pre-stimulus activity while walking indicates that locomotion reshapes sensory readiness and its coupling to early visual responses—consistent with the view that vN serves as a tunable gating signal aligning visual cortices to expected, task-relevant input so that visuomotor mappings remain efficient under dual-task constraints (Di Bello et al., 2025).

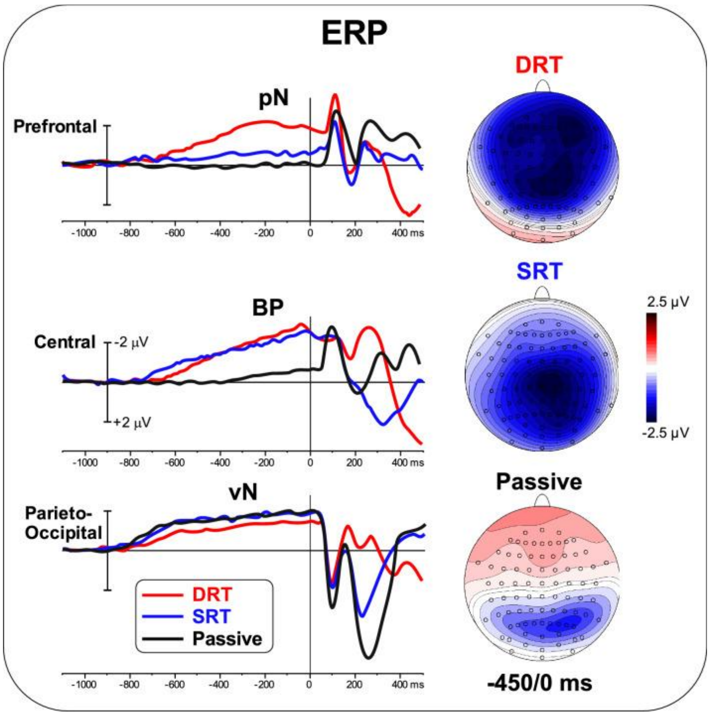
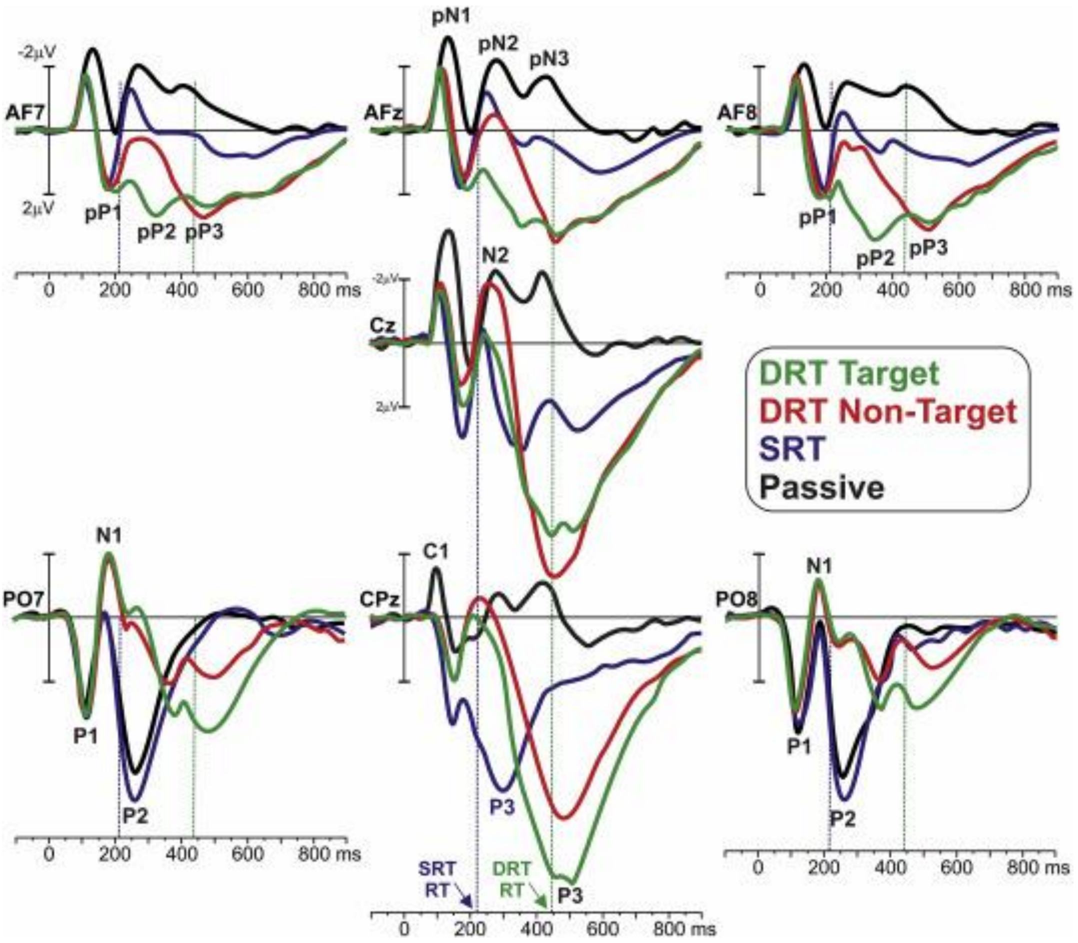


Fig. 3: Example of pre-stimulus waveform and topographic distribution in three different conditions: a DRT task, a SRT task and a passive vision

5.3.7. Post-stimulus components

Among main post-stimulus components, in addition to those already mentioned, the pN1, pP1, and pP2 stand out.



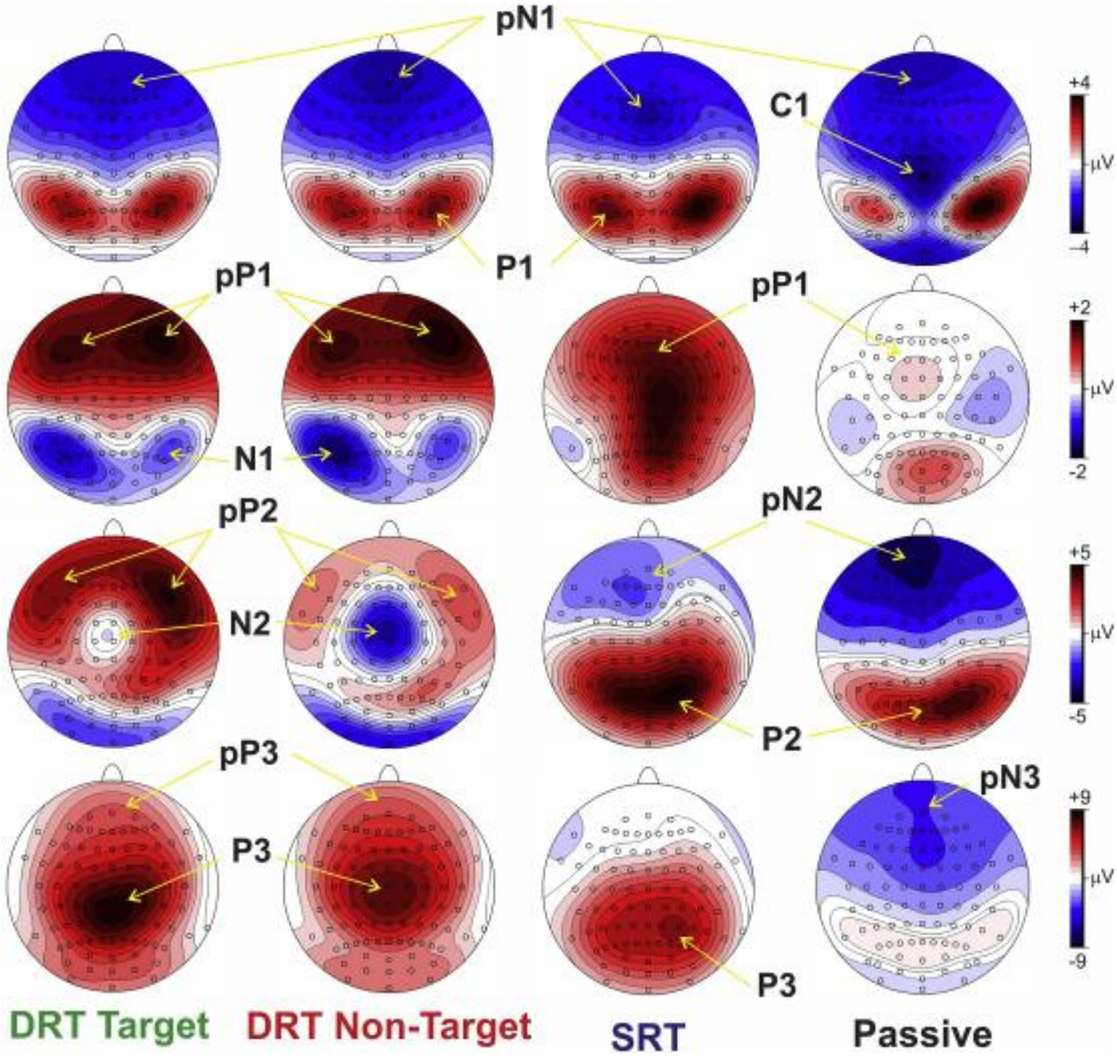


Fig.4: Typical post-stimulus waveform and topographic distribution in three different conditions: a DRT task, a SRT task and a passive vision

The pN1 is an early negative post-stimulus deflection recorded over anterior/prefrontal electrode sites that typically falls within the early sensory-processing window, approximately 80–200 ms post-stimulus, broadly co-occurring with occipito-temporal N1/P1 activity) and—critically—has been localized by source analyses to the anterior insular region and adjacent ventrolateral prefrontal territories (Di Russo et al., 2019; Perri et al., 2018). Functionally, pN1 is interpreted as an index of early perceptual awareness / endogenous perceptual gating within a prefrontal–insular network that detects and flags behaviorally relevant sensory events for subsequent sensorimotor transformation (Perri et al., 2018; Di Russo et al., 2016; Di Russo et al., 2019). In the multisensory domain, pN1 amplitude and timing are modulated by the preparatory, modality-specific state of the system (i.e., modality-specific sensory readiness) and by the presence of congruent cross-modal cues, consistent with anticipatory multisensory integration frameworks: preparatory slow potentials bias insular responsiveness and thereby alter the pN1 generated once the stimulus arrives (Bianco et al., 2019; Bianco et al., 2020; Fiorini et al., 2021). Empirically, task complexity and perceptual load increase pN1 (and early insular activity) when endogenous perceptual analysis must be strengthened (Mussini et al., 2020), while sustained spatial attention selectively enhances pN1 amplitude when attention is directed to the stimulus location (Berchicci et al., 2019). Under dual-task or high cognitive-load conditions, pN1 shows systematic modulation (amplitude and latency shifts) consistent with resource competition: greater concurrent demands attenuate or delay pN1 when perceptual analysis must share limited prefrontal/insular resources, whereas paradigms that promote proactive preparation (strong pre-stimulus readiness) can preserve or even amplify pN1 as a compensatory mechanism (Quinzi et al., 2019; Mussini et al., 2020). During walking / mobile states, mobile-EEG/MoBI studies report that early sensory markers (e.g., N1) are sensitive to locomotor state (walking can either preserve, amplify, or sometimes leave early components unchanged depending on speed, sensory context, and artifact removal); movement-related changes in pre-stimulus oscillatory state (e.g., reduced alpha) predict N1/pN1 amplitude changes, indicating that locomotion alters the baseline preparatory state that gates pN1 generation (Gramann et al., 2010; Malcolm et al., 2017; Chen et al., 2022). In sum, pN1 is best conceptualized as an anterior-insular marker of early perceptual salience and sensory-gating whose amplitude and latency reflect the current modality-specific readiness and multisensory context (Bianco et al., 2019, 2020), the allocation of limited prefrontal resources under dual-task pressure (Mussini et al., 2020; Quinzi et al., 2019), and state-dependent changes introduced by locomotion (Chen et al., 2022).

The pP1 is a positive ERP peak of prefrontal/anterior insular topography that typically peaks in the late early window (commonly reported ≈160–200 ms post-stimulus; Perri et al., 2019) and has been localized—via EEG source and simultaneous EEG–fMRI work—to anterior insular cortex and nearby opercular/ventrolateral prefrontal regions, co-occurring temporally with occipito-parietal early visual components but functionally dissociable as a prefrontal sensory-motor awareness signal (Di Russo et al., 2019; Perri et al., 2018; Ragazzoni et al., 2019). Mechanistically, pP1 indexes early conscious sensory-motor awareness and the initial mapping of perceptual features onto potential action plans; its amplitude scales with perceptual complexity and the requirement for endogenous, insula-mediated re-analysis of stimulus structure (Perri et al., 2019; Mussini et al., 2020). In the context of multisensory integration, pP1 shows sensitivity to the anticipatory multisensory state and to cross-modal congruence: when preparatory potentials bias processing toward a given modality or when congruent multisensory cues arrive, pP1 amplitude is larger and its latency can be shortened, consistent with an insular role in binding sensory evidence into an actionable representation (Bianco et al., 2019; Fiorini et al., 2021). Concerning dual-task and task complexity, pP1 behaves as a “frontline” index of how much perceptual-to-motor transformation capacity the system dedicates to stimulus analysis: complex discriminations or increased categorization demands produce larger pP1 (and pP2) amplitudes (Perri et al., 2019; Mussini et al., 2020), whereas concurrent secondary tasks that siphon pro-active resources can reduce pP1 (or delay its peak) and lead to downstream changes in decision latencies (Quinzi et al., 2019; Mussini et al., 2020). Regarding walking, MoBI evidence indicates that locomotor state modulates pre-stimulus baseline and early sensory processing (changes in alpha, and N1/P1 dynamics), and therefore pP1 is expected to reflect the interaction between sensory availability during gait and insular gating: walking can alter pP1 indirectly through changes in baseline excitability and cross-modal weighting rather than by shifting its generator locus (Gramann et al., 2010; Chen et al., 2022). Finally, source-level and EEG–fMRI studies from the Di Russo group consistently position pP1 within an anterior-insular / ventrolateral prefrontal network that mediates early awareness and the sensory-motor transformation needed for rapid visuomotor behavior (Perri et al., 2018; Di Russo et al., 2016, 2019).

The pP2 is a later prefrontal positive component, commonly reported around 300–350 ms post-stimulus, associated with higher-order stimulus-response (S-R) mapping, decision evolution, and the final commitment to motor output (Perri et al., 2019; Di Russo et al., 2019). Source localization converges on the anterior insula (bilateral, often right-dominant) as a major generator of pP2, consistent with insula involvement in integrating sensory evidence, salience, and motor plans (Ragazzoni et al., 2019; Perri et al., 2018). Neurophysiologically, pP2 amplitude and latency index the strength and time-course of stimulus- response mapping: increases in perceptual complexity or decision uncertainty boost pP2 amplitude and/or prolong its latency, reflecting greater insular recruitment for evidence accumulation and S-R translation (Perri et al., 2019; Mussini et al., 2020). Importantly, spatial-orienting manipulations that affect earlier prefrontal components (pN1/pP1) do not necessarily modulate pP2 (Berchicci et al., 2019), which suggests that pP2 indexes a subsequent, computational stage (mapping/decision) that is partly independent from early perceptual-awareness gains. In dual-task or high-interference situations, pP2 is a sensitive marker of cognitive-motor interference: when a secondary task taxes central decision resources or when walking imposes sensorimotor demands, pP2 amplitude typically decreases and latency lengthens, paralleling degraded behavioral accuracy or prolonged reaction times (literature on dual-task and mobile EEG indicates consistent reductions/latency shifts in later decision-related ERPs under concurrent motor load; Malcolm et al., 2017; Chen et al., 2022). Mechanistically, the Di Russo group frames pP2 as the prefrontal/insular signature of the perceptual-to-decisional stage that gates motor commitment: its modulation by perceptual load, task complexity, and motor state (walking) reflects the integrative operations that bind sensory evidence, attentional priority, and action selection into a final response command (Di Russo et al., 2016, 2019; Perri et al., 2019; Ragazzoni et al., 2019).

Experimental Part

6 Modulation of anticipatory brain activity as function of action complexity

6.1. Introduction

Voluntary actions can be defined as the materialization of thought through movement and massively involve the brain from sensory to cognitive and motor areas (e.g., Flanders 2009). Most of this brain activity occurs well before the movement onset, during action preparation. Deciphering the neural mechanisms underlying the action preparation has been a persistent challenge in cognitive neuroscience. (e.g., Nguyen, Breakspear & Cunnington, 2014). Thanks to their high temporal resolution, one of the best ways to study brain activity related to a movement or stimuli requiring motor responses, is using electroencephalographic (EEG) recordings and event-related potentials (ERP) measures (e.g., Kornhuber & Deecke, 1965; Shibasaki & Hallett, 2006).

Indeed, there is a wealth of scientific evidence in the literature highlighting the role of specific ERP components in cognitive-motor anticipation. Among these, the Bereitschaftspotential (BP), the lateralized readiness potential (LRP), and contingent negative variation (CNV), localized in premotor and motor brain areas, have provided valuable insights into the timing and neural mechanisms underlying movement preparation and execution. These ERPs may appear in different experimental contexts, highlighting their relevance in the study of voluntary and anticipatory motor processes (Brunia et al., 2012). Recent research has further explored the nuances of these pre-movement potentials, highlighting their role in understanding the cognitive role in motor control (e.g., Gentsch et al., 2016; Ody et al., 2023; Reznik et al., 2018). In particular, this anticipatory activity may aid cognitive processing by priming the brain for upcoming movements or events and optimizing. In this context, the BP response selection in accordance with contextual demands (e.g., Kornhuber & Deecke, 2016; Di Russo et al. 2019). Anticipatory activity is also related to motor prediction (e.g., Reznik et al., 2018; Vercillo et al., 2018; Wen et al., 2018), and may represent top-down attentional control (e.g., Di Russo et al. 2019).   In this context, the BP, besides reflecting the necessary motor preparation for the upcoming action, has been described as having a bi-phasic trend with an early and a late phase (e.g., Shibasaki & Hallett, 2006). While the early phase has been described as an unspecific generic preparation associated with the intention to move (e.g., Schurger et al., 2021; Shibasaki, 2012), a specific preparation of the movement is deployed in the later phase to allow last-minute changes and enable learning, to improve performance (e.g., Deecke 2012; Dennet 2005; Mele 2007). In speeded cognitive tasks, the late BP amplitude has been associated with response times (e.g., Di Russo et al., 2019). For more complex movements such as reaching, grasping, or pantomimes, additional activity in the posterior parietal cortex (PPC) has been found in a few studies (Bozzacchi et al., 2012; Wheaton et al., 2005a,b) and named posterior BP (pBP).

Voluntary actions can be executed in response to either external stimuli (here called stimulus-driven actions) or internal decisions (here called self-paced actions). While preparatory ERP associated with self-paced actions has been widely studied for many types of movements, from simple finger flexion to complex praxic movements, (e.g., Shibasaki & Hallett, 2006) including jumping into an abyss (Nann et al., 2019), ERP preceding stimulus-driven actions has been less investigated and, if any, only for tasks requiring just a finger flexion (a keypress) as responses (for a review, Di Russo et al. 2017). However, the LRP, which reflects the activation of response-related processes in motor cortex succeeding stimulus-related processing (e.g., Masaki, Wild-Wall, Sangals, & Sommer, 2004), was found larger for complex as compared to simple responses (Hackley and Miller, 1995; Stief, Leuthold, Miller, Sommer, and Ulrich 1998). These studies associated this complexity effect to the need of parallel programming for multiple effectors; however, they used hands responses only and no information on premotor and other anticipatory brain areas is available.

Studies investigating the preparatory activity of stimulus-driven actions (in addition to the BP) reported two other components called prefrontal negativity (pN) and visual negativity (vN). The pN has been localized in the inferior prefrontal gyrus and has been associated with cognitive preparation intended as top-down cognitive control (mainly attentional and inhibitory) for upcoming actions (e.g., Berchicci et al., 2020). Specifically, in the context of a discriminative perceptual task, decisions can be seen as the result of a continuous accumulation of sensory information from a baseline point until a threshold is reached (Ratcliff, 1978). Rapid decisions are more prone to error, whereas cautious responses require more time (Wenzlaff et al., 2011); this phenomenon is known as the response accuracy/speed trade-off (SAT) (Bogacz et al., 2006). In this vein, the BP and the pN have been described as a form of accelerator/braking system based on predictive internal models able to modulate the SAT performance (Di Russo 2019; Perri et al.,

2014) and to regulate the behavior proactively before the event (e.g., Aron, 2011). In speeded discriminatory response tasks (response time <500 ms), prefrontal and premotor areas interact with each other to proactively optimize the speed/accuracy trade-off (e.g., Perri et al 2014) using a proactive accelerator/brake (excitation/inhibition) system where the premotor area is the accelerator and the prefrontal area is the brake which is released (such as in a muscle car burnout) when the target trial (the green light in the muscle car example) is detected (Di Russo et al., 2019). The vN has been localized in the extrastriate visual areas and has been associated with the visual readiness reflecting top-down signals from sensory visual areas for the allocation of preparatory sensory resources for upcoming tasks (e.g., Bianco et al., 2020). The pN and the vN were just described in tasks requiring simple movements (finger flexion) and have not yet been studied for more complex movements performed by upper or lower limbs, such as reaching or walking/stepping, respectively. For a detailed description of these components based on a large sample see Di Russo et al. (2019).

Overall, all this evidence suggests that the brain activity preceding voluntary movements involves cortical networks in anterior premotor and prefrontal areas but also in more posterior parietal and occipital regions. The contribution of the PPC preparatory activity for stimulus-driven actions has been widely investigated in both human and animal models (e.g., Sulpizio et al., 2023). In macaque, several studies (e.g., Fattori et al., 2009) have shown that neurons in the PPC become active well before the appearance of any electromyographic movement-related activity, thus confirming the role played by these areas in the planning of reaching (e.g., Batista & Andersen, 2001; Cui & Andersen, 2007). As repeatedly demonstrated, in humans the PPC is considered a main substrate for reach and walk planning, that is whole body actions performed using both upper and lower limbs (e.g., Pitzalis et al., 2019; Sulpizio et al., 2020).

Based on the mentioned data, this study was born from the question of whether in cognitive tasks the greater the response movement complexity, the greater the need to integrate information of different nature to perform it, so the greater the activity in a specific functional circuit involved in the movement planning. Therefore, we aimed at verifying which pattern of brain activity is associated with the preparation of stimulus-driven actions requiring increasing levels of motor complexity.

Complexity can be defined by the number of dimensions involved in motor activity (e.g., Cordo & Gurfinkel, 2004). Here movement complexity was defined by the number of muscle districts involved in the movement, under three different conditions. Specifically, the motor complexity was manipulated by asking participants to provide their response by a simple keypress (finger flexion) or by adding additional movements such as long-range reaching movement alone or in combination with a standing stepping movement. Thus, we designed three task conditions (Keypress, Reaching, Reaching-Stepping) with identical visual and cognitive task complexity (50/50 Go/No-go task) but with a different motor engagement.

Using this experimental design and specific comparison across conditions, we sought to identify the preparatory cortical activity involved in cognitive task requiring increasing motor complexity of the response. The expectation is to identify modulation in amplitude and timing of the BP, pBP, pN, and vN components, as a function of the required involvement of premotor, parietal, prefrontal, and visual areas preparatory activity, required by the three conditions, respectively. We specifically expect that, at the least, the early BP should be similar for all movements since the intention to move should be common (e.g., Lau et al., 2004). The reaching preparation should be characterized by the pBP specifically involved in that kind of action (e.g., Cui & Andersen, 2007). Since stepping require reaching and a whole-body movement toward the front space, the preparation should be dominated by medial PPC activity and visual-related readiness (the vN) for the management of the front space (Berchicci et al., 2020; Piserchia et al., 2017). To test these predictions in depth, in addition to scalp activity, intracranial activity in the parietal and occipital areas has been reconstructed using source localization methods.

Secondarily, since several studies found that the BP amplitude is associated with the response time, but used simple keypress responses only (e.g., Bianco et al., 2020; Di Russo et al., 2019; Mussini et al., 2023; Perri et al., 2014; Starr et al., 1995), we also tested if this correlation is present for more complex responses.

6.2. Methods

6.2.1. Participants

For the determination of the sample size, the G*Power 3.1.9.7 software (Faul et al., 2009) was used. A priori power analysis was used to obtain a minimum power of 0.90, as effect size was selected f=0.338 taken from the minimum partial eta squared of Bianco et al. (2020) results, which used a similar ERP design. The other settings were the following: α=0.05, number of measurements=6, correlation among repeated measures=0.50 and, non-sphericity correction □=1.

This calculation resulted in a recommended minimum sample size of 19 for within-factors repeated measures analyses of variance (ANOVA) used for ERP analyses. After these calculations, 19 volunteers participated in the study (mean age 23.2 years ±1.3, 5 females, 14 males). As inclusion criteria, all participants were healthy having no history of neurological, psychiatric, or chronic somatic problems. The participants did not take medication during the experimental sessions and had normal or corrected-to-normal vision. All participants were right-handed. Before the experimental procedure, each participant was informed about all procedures and was asked to sign an informed consent. The procedures followed the Declaration of Helsinki guidelines and were approved by the committee for the authorization of the research (CAR) at the University of Rome "Foro Italico".

6.2.2. Stimuli and procedure

The experiment was done in the Cognition and Action Neuroscience Laboratory at the University of Rome "Foro Italico". Participants were tested in a low-lit, sound-attenuated room after an EEG cap was mounted on the scalp. They were placed in front of a computer screen 170 cm from their eyes.

Participants performed during the EEG recording a discriminative response task (DRT), i.e., a Go/No-go paradigm. A yellow fixation point (diameter 0.15°) on a black background was present in the center of the screen throughout the whole experimental session. Four visual stimuli (i.e., square configurations subtending a side of 4° and consisting of vertical and/or horizontal bars) were randomly visualized for 250 ms with equal probability; the stimulus–onset asynchrony varied from 2200 to 3200 ms to prevent stimulus prediction and ERP overlaps with previous and following stimuli. Two target and two non-target stimuli were used (instead of one target and one non-target) to allow a cognitive load sufficiently high to produce a robust pN component (Di Russo et al., 2019).

Participants had to press the button with the right index finger as soon as possible only when (two out of four) designated 'Target' stimuli (Go) appeared on the screen, while they had to withhold the motor response when 'Non-target' stimuli (No-go) appeared; the experimenter equally emphasized speed and precision. Figure 1a shows a schematic representation of the stimuli and the timing. The order of presentation of the four stimuli was randomized between runs. The duration of each run was 2 min and 15 s with a pause interleaved. Ten runs for three conditions were administered allowing to collect 400 trials for each stimulus category (target and non-targets) in approximately 70 min, depending on the individual rest time during pauses.

The experimental session included three task conditions (Figure 1b) all requiring the keypress by the right index finger as a response. The conditions were executed in separated randomly intermixed blocks. In the simple Keypress condition, participants were seated in a comfortable chair facing a desk with a response pad on top at 30 cm from the body. They were asked to complete the DRT with minimal motor involvement, with the right hand always placed on the response pad, they had to press a green key just flexing the right index. In the Reaching condition, participants were seated as in the Keypress condition, but the response pad was positioned at 50-55 cm away from the body requiring a full arm extension to reach and press the green key (i.e., long-range arm reaching movement). The response pad distance varied based on the length of the participant’s arm. After the keypress, the participant had to return to the resting position, with both hands on the desk close to the body. In the Reaching-Stepping condition, participants stood at 75-80 cm from a 130 cm tall pod with the response pad on top. They were required to take a step and extend the right arm to reach and press the green key and then come back in the rest position with the legs slightly apart and the arms at the sides. The step consisted in bringing the right leg forward, while the left one remained stationary.

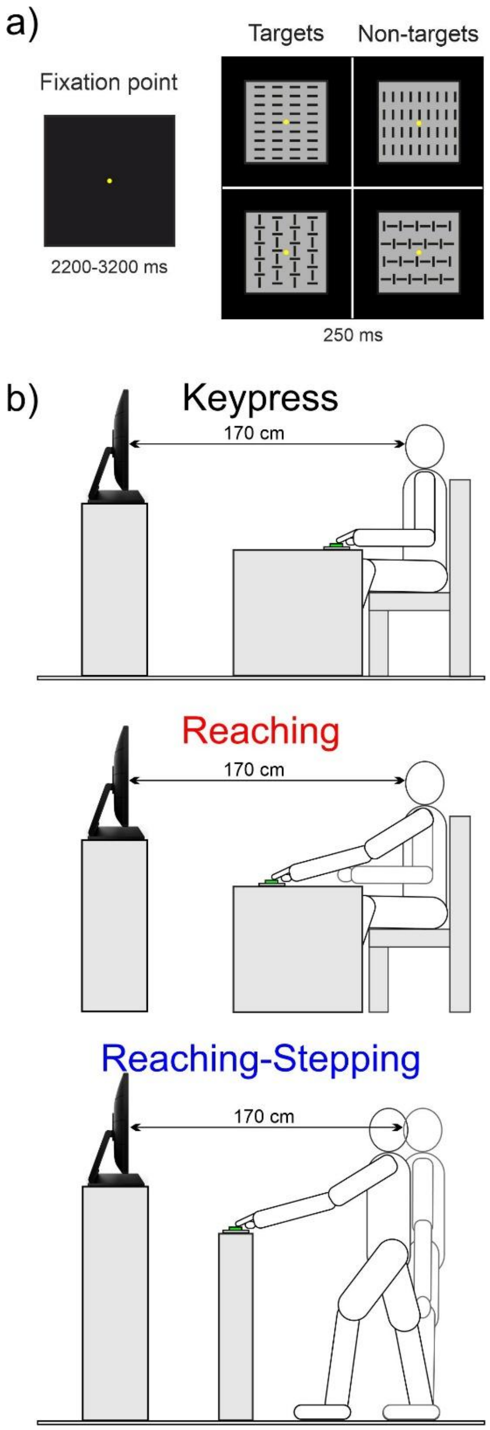


Figure 1. a) Representation of the Target (Go) and Non-target (No-go) stimuli used in the tasks and their durations. b) Schematic representation of the participant's motor involvement and body position during the three task conditions.

6.2.3. Behavioral data

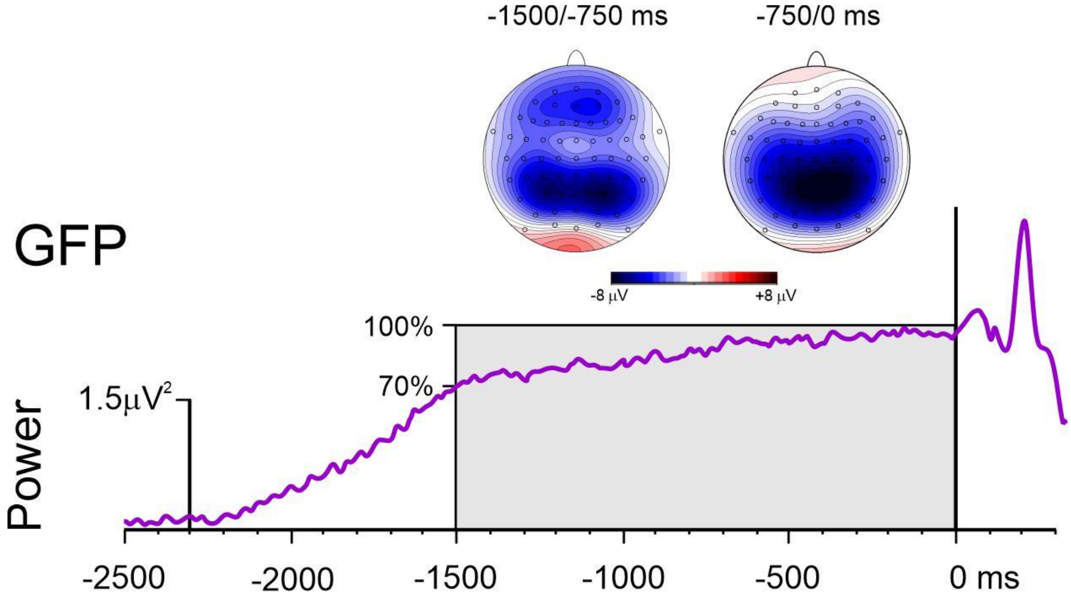
The response speed was assessed using the response time (RT) for correctly executed trials. Response accuracy was assessed by summing the erroneous responses to non-target stimuli and the omitted responses to target stimuli, this value has been expressed in percentage (Err%).

6.2.4. EEG recording and analysis

All participants were tested using a 64-channel EEG system (Brainamp^{TM} amplifiers) with active electrodes (Acticap^{TM}) and software (Recorder 1.2 and Analyzer 2.2) all by Brain Products GmbH (Munich, Germany). The electrodes were mounted according to the 10–10 International System and referenced to the averaged mastoids (TP9, TP10). Horizontal and vertical electrooculograms (EOG) were monitored by additional bipolar recordings. The EEG was digitized at 250 Hz, amplified (bandpass of 0.01–60 Hz including a 50 Hz notch filter), and stored for offline averaging. The signal was then filtered with 0.1 Hz high-pass and 40 Hz low-pass filters.

To investigate the pre-stimulus activities (independently from the stimulus category), the signal was segmented in epochs starting 2500 ms before the stimulus onset (time 0) and lasting for 2800 ms. Eye movement artifacts were corrected using the Independent Component Analysis (ICA) ocular correction Infomax algorithm: it has been shown that this method, introduced by Jung et al. (2000), revealed better results than other ocular correction methods (e.g., Hoffmann & Falkenstein, 2008). Furthermore, semi-automatic artifact rejection was performed before signal averaging to discard epochs contaminated by signals exceeding the amplitude threshold of ±80 µV, and about 3.9% of trials were rejected. The artifact-free trials were averaged, and pre-stimulus activities were measured with respect to a −2500/-2300 ms baseline. Given that the stimulus category was unpredictable at the pre-stimulus phase, target and non-target trials were averaged. Only trials with correct responses were considered.

For the intervals and electrodes to be included in statistical analysis, the “collapsed localizer” method was utilized (Luck & Gaspelin, 2017). Accordingly, a localizer ERP was obtained by collapsing (averaging) all the considered groups and conditions. As shown in Supplemental Figure 1, the global field power (GFP) was calculated to select the analysis interval. The GFP describes the ERP spatial variability considering all scalp electrodes and allowing a reference-independent descriptor of the ERP. As done in the past for similar pre-stimulus ERP (e.g., Mussini and Di Russo 2022), the interval in which the GFP was larger than 70% of its maximum value was used for further analysis. This value reasonably allows us to select the more reliable pre-stimulus activity. The approach designated an interval from ~-1500 to 0 ms which was divided into two equal parts in order to consider both early and late activity. The mean amplitude of these two intervals (-1500/-750 ms, -750/0 ms) was calculated for statistical analysis. The electrodes with an amplitude larger than 70% of the maximum value in that interval were collapsed in spatial pools and considered for statistical purposes. As shown in Supplemental Figure 1, Four foci of medial activity were present: prefrontal (pN), central (BP), parietal (pBP), and occipital (vN). The pN was therefore represented by a pool of electrodes including Fp1, Fpz, Fp2, AF3, AFz, and AF4. The BP was represented by a pool including C1, Cz, C2, CP1, CPz, and CP2 electrodes (central pool). The pBP was represented by P3, P1, Pz, P2, P4. The vN was represented by PO1, POz, PO2, O1, O2.



Supplemental Figure 1: Global field power (GFP) calculated on the ERP average of the three conditions. To consider a reasonable interval for the statistical analysis, 70% of the maximum pre-stimulus power was taken. The topographical maps of the -1500/-750 and of the -750/0 ms intervals are also shown.

To isolate the preparatory activity associated with reaching, the ERP of the Keypress condition was subtracted from the ERP of the Reaching condition. In addition, to isolate the preparatory activity associated with stepping, the ERP of the Reaching condition was subtracted from the ERP of the Reaching-Stepping condition. Based on these differential ERP activities, the source localization of these waveforms (in the -1500/0 ms whole pre-stimulus period) was realized using the “exact low-resolution brain electromagnetic tomography” (eLORETA) software (freely available at www.uzh.ch/keyinst/loreta.htm) to compute the cortical three-dimensional distribution of current density. This method utilizes a discrete, three-dimensional distributed, linear, weighted minimum-norm inverse solution. The weights applied in eLORETA confer precise localization capabilities to test point sources, generating current density images with exact localization, albeit with a limited spatial resolution (i.e., neighboring neuronal sources exhibit high correlation). Notably, eLORETA demonstrates no localization bias, even in the presence of structured noise, representing an advancement over LORETA and its standardized version, sLORETA (Pascual-Marqui, 2002). For this source analysis, we focused on parietal and occipital areas to verify the prediction made on these areas in the introduction section. We have chosen to consider the whole period since preliminary analysis made separately on the two intervals (-1500/-750 ms and -750/0 ms) yield comparable results and therefore did not add information.

6.2.5. Statistical analysis

After checking for normality and homoscedasticity of the distribution of the variables, for the behavioral data we performed a one-way repeated measures analysis of variance (ANOVA) with the Condition factor at three levels (Keypress, Reaching, Reaching-Stepping). For ERP data, we used a 3x2 repeated measures ANOVA with the Condition factor (Keypress, Reaching, Reaching-Stepping) and Interval (early, late) factor. The alpha threshold was set to 0.05. The partial eta squared (η_p^2) was reported as a measure of effect size. The Bonferroni post-hoc test was used to compensate for the multiple comparisons. We also tested the correlation between the BP amplitude and the RT to confirm previous studies (e.g., Bianco et al., 2020; Di Russo et al., 2019; Mussini et al., 2023; Perri et al., 2014; Starr et al., 1995). The Statistica 11 software (StatSoft Inc., Tulsa, OK, USA) was used for statistical analysis.

6.3. Results

6.3.1. Behavioral data

The ANOVA on the RT showed a significative difference among the three conditions ($F_{(2,36)}=159$, $p<0.001$, $\eta_p^2=0.898$). Post-hoc comparisons showed shorter RT ($p<0.001$) in Keypress condition (549 ms ±49) than Reaching (1026 ms ±175) and Reaching-Stepping (1238 ms ±234). The RT in the latter conditions did not differ ($p=0.122$).

The ANOVA on the Err% showed no significant effect of Condition ($F_{(2,36)}$=0.8, p=0.462, $\eta_p{}^2$=0.042). The error rate was low being 1.8% ±0.9, 1.9% ±1.2 and, 1.3% ±0.8 in Keypress, Reaching, Reaching-Stepping conditions, respectively.

6.3.2. ERP data

ERP activity initiated about 2000 ms before stimulus onset. Negative slow ramps were present in different scalp areas with different slopes and shapes and were maximal at stimulus onset (Figure 2a). This wide negativity was present in the medial prefrontal (the pN), central (the BP), parietal (the pBP), and occipital (the vN) areas as shown by scalp topography (Figure 2b). In the early interval, the distribution was posteriorly located (the vN), especially for the Reaching-Stepping condition. In the late interval, the topography was anteriorly located extending in the prefrontal areas in the Keypress condition (the pN). The central distribution was present in all conditions (the BP), however, in the late interval of the Reaching condition was posteriorly located peaking at parietal sites (the pBP). The pN was visible in the Keypress condition only.

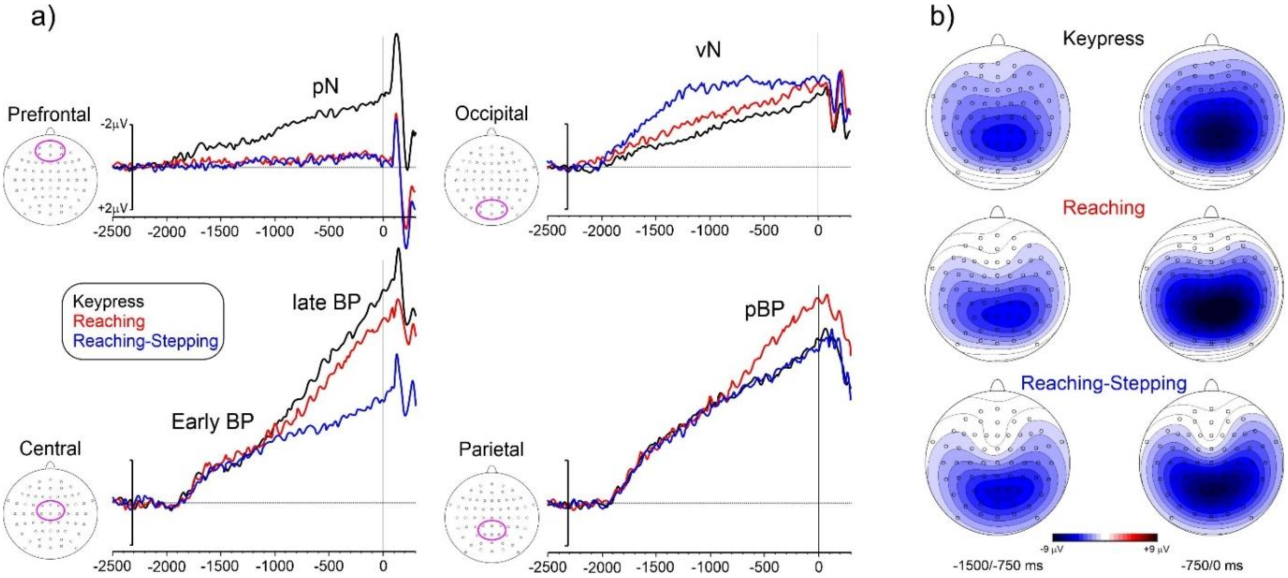


Figure 2: a) Pre-stimulus ERP waveforms in the three conditions at the prefrontal, central, parietal, and occipital areas electrode pools. These regions are highlighted in the head representation on the left of the relative waveforms. The associated ERP components are labeled. b) Scalp topography (top-flat view) of the three conditions in the -1500/-750 ms and -750/0 ms intervals.

As showed in Table 1. The ANOVA on the Prefrontal pool showed a significant effect of Condition, Time, and their interaction. Post-hoc comparisons on the interaction indicate that the pN amplitude in the Keypress condition, for both intervals, was larger (all p<0.001) than in the

Reaching and Reaching-Stepping conditions, which did not differ from each other (p=0.446). ANOVA on the Central pool showed a significant effect of Condition, Time, and their interaction. Post-hoc comparisons on the interaction indicate that the early BP amplitude did not change among the three conditions (all p>0.229). Still, in the late interval, all the conditions were significantly different (all p<0.01) with the largest amplitude for the Keypress condition, lowest for the Reaching-Stepping, and intermediate for the Reaching condition (p<0.001). ANOVA on the Parietal pool showed a significant effect of Time and of the interaction. Post-hoc comparisons on the interaction indicate that the early pBP amplitude did not change among the three conditions (all p>0.310), but in the late interval, the Reaching condition showed larger amplitudes (p=0.004) than the other two that did not differ from each other (p=0.431). ANOVA on the Occipital pool showed a significant effect of Condition, Time, and their interaction. Post-hoc comparisons indicate that the vN amplitude in the Reaching-Stepping condition, for the early interval, was larger (p=0.002) than in the Reaching and Keypress conditions, which did not differ from each other (p=0.378). In the late interval, the Reaching-Stepping condition amplitude was larger than the Keypress condition (p=0.023), but not than the Reaching condition (p=0.078). Figure 3 shows the mean amplitudes of the interactions.

The correlation between the BP amplitude and the RT was significant for the keypress condition (r=0.43, p=0.024), but it was not significant for the reaching (r=0.21, p=0.312) and the reaching stepping (r=0.17, p=0.451) conditions.

Prefrontal (pN)	**DoF**	**F**	**p**	**η_p^2**
Condition	2, 36	10.7	<0.001	0.373
Time	1, 18	11.3	0.003	0.284
Condition x Time	2, 36	6.5	0.004	0.265
Central (BP)				
Condition	2, 36	8.2	0.001	0.274
Time	1, 18	14.7	0.001	0.584
Condition x Time	2, 36	4.6	0.017	0.202
Parietal (pBP)				
Condition	2, 36	3.1	0.057	0.110
Time	1, 18	96.3	<0.001	0.843
Condition x Time	2, 36	7.0	0.003	0.279
Occipital (vN)				
Condition	2, 36	7.0	0.003	0.407
Time	1, 18	7.8	0.016	0.295
Condition x Time	2, 36	7.4	0.002	0.289

Table 1: ANOVA data of ERP components amplitude comparisons. Degrees of freedom (DoF). Partial eta squared (η_p^2). The significant effects are highlighted in red.

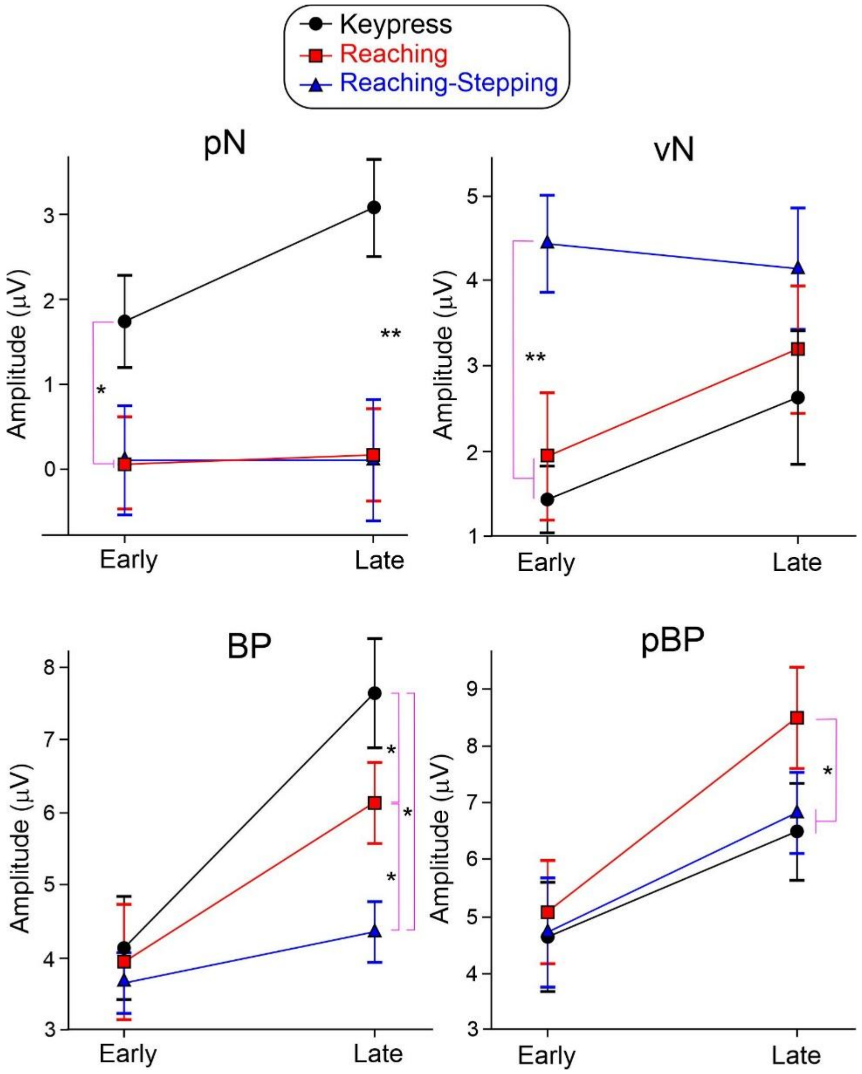


Figure 3: Mean and standard deviation of the interactions between Condition and Time factors for the ANOVAs on each component. *p<0.5 **p<0.01

6.3.3. Difference ERP waves

In order to examine variations in the brain regions responsible for organizing the different actions in our task, we calculated differential waves by subtracting the ERP of the simpler condition from the more complex. Figure 4 shows the results of the differential waves that highlight the left parietal contribution in the reaching preparation and the bilateral medial parieto-occipital contribution of the stepping preparation. Figure 4a shows the scalp topography of the voltage distribution from a posterior point of view in the -1500/0 ms interval of the Reaching minus Keypress difference wave (left) and of the Reaching-Stepping minus Reaching difference wave. Figure 4b shows, for the same difference wave and interval, the source reconstruction of those ERP activities. Source analysis for the Reaching minus Keypress difference shows that the activity was localized almost exclusively in the left hemisphere, which is the hemisphere contralateral to the right arm/hand used to perform the task. In addition, it suggests that this reaching-related activity mainly originates latero-posteriorly and dorsally up to the anterior precuneus but not medially. Source analysis for the Reaching-Stepping minus Reaching difference shows that the activity was mainly bilateral and that the stepping-related activity originates in the IPL and the PPC, both medially and dorsally up to the anterior precuneus. In addition, ERP activity may originate also latero-posteriorly from the middle occipital gyrus but mainly in the right hemisphere. Supplemental Figure 2 reports the same source analyses performed on the unsubtracted data from the three conditions. This data indicated that the activity for the reaching and reaching-stepping conditions involves the parietal-occipital regions more than that observed in the simple keypress condition.

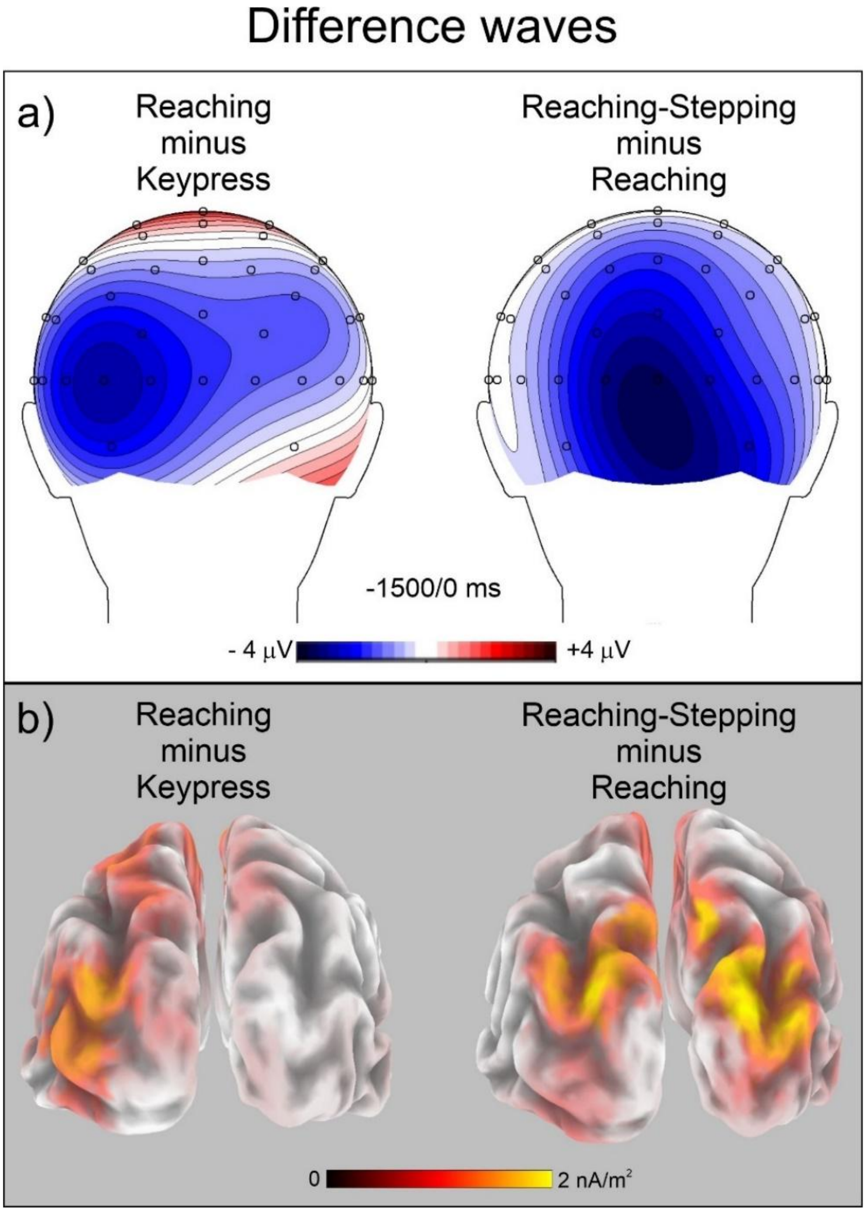
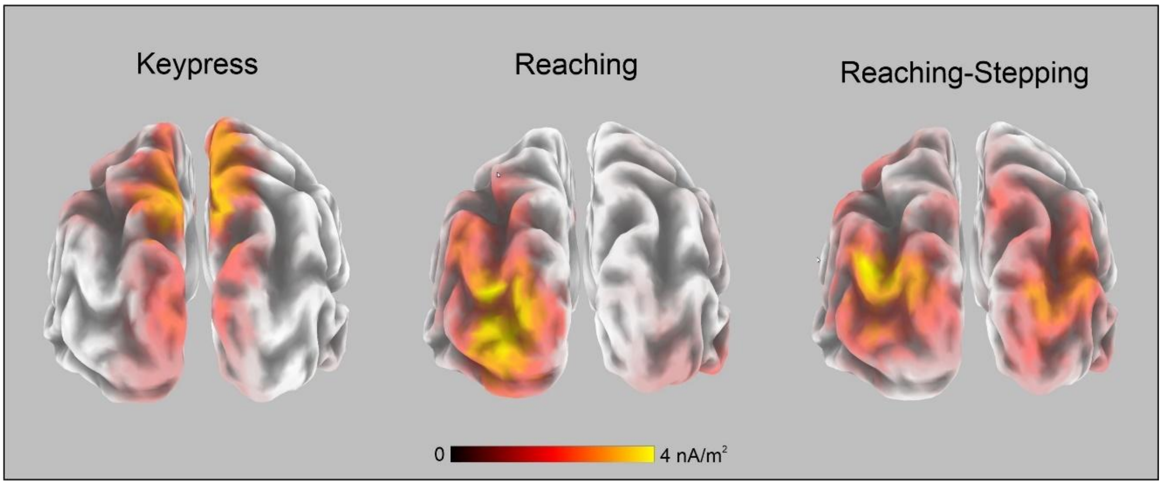


Figure 4: Differential ERP waves. a) Scalp topography of the Reaching minus the Keypress condition (left) and of the Reaching-Stepping minus the Reaching condition (right) in the -1500/0 ms interval. b) Source analyses of the two differential waves in the same interval. The head and the brain representations are in the posterior view.



Supplemental Figure 2: Source analyses of the unsubtracted ERP of the three conditions in the -1500/0 ms interval. The brain is in the posterior view.

6.4. Discussion

This study aimed to identify possible different patterns of brain activity associated with the anticipation and planning of three different stimulus-driven actions with an increasing level of complexity in terms of body segment involvement. This is because previous studies on anticipatory ERP waves just used keypress as response movements (e.g., Brunia et al., 2012; Ody et al., 2023; Schurger et al., 2021). Results showed that although all actions required similar early premotor and parietal activities, three different patterns of later brain preparation preceding each different type of action were identified.

6.4.1. Keypress condition

The preparation of a simple finger keypress strongly involved prefrontal (the pN) and premotor (the BP) areas and less parietal (the pBP) and occipital areas (the vN). This result supports the literature that extensively uses this simple motor response in cognitive tasks and showing that the prefrontal and premotor areas interact to proactively optimize the speed/accuracy trade-off (e.g., Perri et al. 2014) as an accelerator/brake system in which the prefrontal area acts as the brake and the premotor area acts as the accelerator. Bogacz (2010) suggests that the SAT is modulated in association with pre-motor areas rather than in sensory or primary motor areas; moreover, the emphasis on response speed increases the baseline firing rate of neurons involved in movement control. Since, in fact, participants were given the instruction to respond as quickly as possible, while avoiding, at the same time, to make mistakes, and since the probability of making errors of commission increases as the time available to provide the response decreases, it follows that the effort to cognitively control the action increases.

Compared to the other conditions, even though it requires more excitatory (larger BP) and inhibitory (larger pN) activity during the preparation phase, the Keypress condition requires less parietal and occipital preparatory activity likely because arm/body movements were substantially absent, so less visual readiness (the vN) is necessary. The large pN may also indicate a large recruitment of inhibitory control in order to execute precise and discrete actions. This confirms previous ERP (e.g., Berchicci et al., 2012) and fMRI studies (e.g., Jaffard et al., 2008) showing the role of the PFC, in synergy with other brain regions, in proactive inhibition. Furthermore, a relevant factor to consider in the Keypress condition is the immediate tactile feedback on the fingertip. Indeed, in this condition, unlike others, participants consistently maintained the finger on the response button. Forster & Eimer (2007) proposed that continuous tactile feedback can enhance motor performance in discrimination tasks, likely by facilitating sensorimotor integration and response preparation. Some ERP studies have shown an increase in somatosensory potentials in response to tactile stimuli during the preparation of both eye movements (Gherri & Forster, 2012), keypress or reaching movements (Eimer et al., 2005; Forster & Eimer, 2007; Baldauf & Deubel, 2009). Similarly, Juravle et al. (2016), comparing ERP between conditions with tactile or visual feedback, found greater involvement of frontal and prefrontal areas in the tactile condition. Therefore, is possible that the large pN and BP for the Keypress condition may be also due to the facilitating role of tactile feedback on task preparation.

6.4.2. Reaching condition

The Reaching condition tested here required strong involvement of parietal and premotor areas, a small contribution from the occipital areas, and no contribution from the prefrontal areas. The dominance of parietal areas (the pBP) in these movements confirms the previous literature indicating that brain activity related to arm-stretching, reaching anticipation, and direction planning (also when the behavior is not effectively carried out) are produced in parietal areas (e.g., Inouchi et al., 2013). The parietal cortex would integrate visual and proprioceptive elements to establish the trajectory of the arm toward the target (Vesia et al., 2008) and the object‘s distance from the body (Pitzalis et al., 2015). The parietal activity observed here (in the difference wave) for visually guided reaching actions was prevalently localized in the left hemisphere, contralateral to the arm used to perform the task. The localization of this activity confirms the previous literature (e,g., Culham et al., 2003), showing that contralateral parietal areas are responsible for hand/arm control during reaching movement. The source analysis showed that this parietal activity is mainly situated dorsally in the anterior precuneus, where the human homologue of macaque area PEc was found (Pitzalis et al., 2019). Although only a few studies have been conducted to specifically investigate the functional role of this region in humans, there is strong evidence in the literature for an important role of this region, and more specifically of the region likely hosting human area PEc, in a set of sensorimotor transformations needed to make a visual pointing toward a visual target on the screen (Pitzalis et al., 2019), or grasp a visually presented object (Sulpizio et al. 2020).

Reaching-related activity was found also in the lateral portion of the occipital lobe, suggesting that the visual brain also plays a role in the cortical network underlying preparatory activity. The role of the occipital areas during movement preparation and execution confirms the action-specific perception theory postulating that perception essentially needed to link the environmental information with our ability to act within it (Witt, 2011; Kline et al., 2020). This is particularly true for action requiring ample movements such as the Reaching and Reaching-Stepping conditions and less for the Keypress condition.

6.4.3. Reaching-Stepping condition

The Reaching-Stepping condition required strong involvement of occipital preparatory activity (the vN) and contributions from the premotor, and the parietal areas. Although this ERP activity preceding stimulus-driven stepping has never been reported before, our results are in line with the previous literature on the same topic. Indeed, several studies have described brain activity associated with stepping planning in the PPC and occipital areas (e.g., Evans et al., 2013; Kline et al., 2020), especially when the walk takes place in an enclosed space (Dalla Volta et al., 2015). A piece of evidence particularly relevant here is the ERP study from Berchicci and coworkers (2020) where participants were asked to step on a platform to investigate motor planning for forward and backward self-paced stepping. Results revealed premotor (during both forward and backward stepping), parietal (mainly during forward stepping), and prefrontal (during backward stepping) contributions. These different activation patterns can be explained by taking into consideration that the backward step is a more complex movement requiring major cognitive control and it can also be considered as an avoiding behavior, demanding inhibition, while the forward step is like an oriented-to-action behavior, a familiar and simple movement towards something, so it mainly requires the analysis of the surrounding space which strongly involves the parietal cortex. Moreover, the occipital activity was not dominant probably because interaction with objects was not required. The present source analysis (in the difference wave) showed that this parietal activity is bilateral and mainly situated dorso-medially in correspondence with cortical regions like the parieto-occipital sulcus (where area V6A is located) and the anterior precuneus (where the human homologue of macaque PEc is located). There is robust evidence in macaque and human literature for the important role of both these regions in a set of sensorimotor transformations needed to make stimulus-driven actions toward a visual target. In particular, the anterior precuneus plays a central role in visually guided locomotion, being implicated in controlling leg-related movements as well as the four limbs' interaction with the environment. Human area PEc (hPEc; Pitzalis et al. 2019) responds to both arm and leg movements (although leg movements elicit stronger activations), is involved in implementing the sensorimotor transformations needed to grasp a visually presented object (Sulpizio et al. 2020), and is connected with somatosensory regions hosting a leg representation (area PE and primary somatosensory cortex). In addition, hPEc shows a sensitivity to self-motion compatible visual stimulation responding to the optic flow; a stimulus that gives the brain the illusion of self-movement when the body is stationary (Pitzalis et al. 2019, 2020). Similarly, to reaching condition, stepping-related activity was found also in the lateral portion of the occipital lobe, mainly on the right hemisphere. Interestingly, evidence from fMRI studies showed that the middle occipital gyrus and the intraparietal-transverse occipital gyrus may both be recruited, along with parietal and frontal areas, during a locomotion-related activity (Dalla Volta et al., 2015) as well as during hand and foot pointing movements (Pitzalis et al., 2019).

6.4.4. Condition comparisons

The comparison among the three conditions showed that the early BP amplitude was similar in the three conditions confirming the BP omnipresence in any voluntary movement (e.g., Nann et al., 2019). The late BP was found to be the largest in the Keypress condition, intermediate in the Reaching condition, and small in the Reaching-Stepping condition. The pN was present in the Keypress condition only. This could be explained because greater cognitive control is needed to inhibit a simple and, therefore, completely automatic movement, but also, by the correlation between the BP amplitude and the response time which was previously reported (e.g., Di Russo et al., 2019) and confirmed here. The correlation between the BP amplitude and RT was not significant for the reaching and reaching-stepping conditions likely because large movement time required by these latter actions. Conversely, the significant correlation with the keypress condition may be due to the practical correspondence of the reaction and the response times since movement time in this condition was negligible. The pBP was found to be larger in the Reaching condition and equally large in the other two conditions confirming its association with finalized arm movements (Breveglieri et al., 2014). Finally, the vN, which has been associated with visual and attentional readiness and the construction of an internal representation of a stimulus aimed at increasing the response speed to the materialization of the stimulus itself (Di Russo et al., 2019, 2021), showed greater amplitude in the Reaching-Stepping condition, followed by the Reaching condition and then the Keypress condition. This is probably because the Reaching-Stepping condition requires body movements to the target and visual anticipation has a key role in body navigation (e.g., Grill-Spector et al., 2001).

6.5. Conclusive Remarks

We found three different patterns of brain preparation preceding three different stimulus-driven movements. We postulated that the key factor of the actions that change how the brain engages in preparation is the different motor complexity between the three tasks. Here we choose to define motor complexity as the number of joints, or the number of muscle districts involved in the movement itself. From this point of view, multi-joint actions (as stepping) present an intrinsic major motor complexity than single-joint actions (as key press) and this represents an effective way of studying the central nervous system in a quantitative and experimentally verifiable manner (e.g., Hogan et al., 1987).

It is also possible that the observed effects are closely related to the specific and different demands of each task. Indeed, the keypress task elicited the largest pN component in the prefrontal area, which could indicate the recruitment of cognitive control resources for precise and discrete actions. The reaching task resulted in an increased pBP component in the parietal area, potentially reflecting the integration of spatial and motor resources necessary for arm movements. The stepping task showed a heightened vN component in the occipital area, supporting the involvement of visual and spatial processing resources that are likely engaged when whole-body movement is required. These findings suggest that each task seems to recruit different neural resources and that the brain's preparation for each task could be tailored to the specific set of demands, from sensory integration to motor planning and execution.

The interpretation based on motor complexity and task demands may be no alternative but complementary key factors of the actions that may change how the brain prepares for it. Both factors should be considered to understand how the allocation of neural resources varies depending on the task demands. To summarize, we found different patterns of preparatory brain activity associated with different actions with increasing levels of complexity and different task demands. All movements required similar early premotor and parietal activities, but while the simple keypress required inhibitory control in prefrontal areas, reaching action required strong hand control in contralateral parietal areas, and stepping action a body movement control in bilateral medial parieto-occipital areas.

Reconstruction of the cortical sources subtending the found ERP confirmed previous neuroimaging literature and proposed the novel notion that the found brain areas are strictly related to action anticipation since they are active well before the movement-triggering stimulus and therefore action initiation. These activities that can be detected in ERP analyses, may enrich the readiness potential literature (e.g., Schurger et al., 2021; Shibasaki e Hallett, 2006) and be used for a better understanding of motor control and the neural processes that support action anticipation in humans.

Finally, is worth noting that the interpretation of the observed ERP components, as direct markers of the activity of the underlying brain regions, represents a limitation of this study. Due to the inverse reconstruction techniques and the limited spatial resolution of EEG, there is some uncertainty in the exact position of the estimated intracranial sources, even if eLORETA source analysis offers a credible estimate of cortical generators. For this, care must be used interpreting correlations between ERP and brain regions. Future research could incorporate complementary neuroimaging methods providing higher spatial resolution.

7. Chapter. Electrophysiological indexes of the cognitive-motor trade-off associated with motor response complexity in a cognitive task

7.1. Introduction

Voluntary movements have different degrees of complexity. Complexity can be defined by the number of dimensions involved in motor activity such as the number of joints involved or the movement degrees of freedom (Cordo and Gurfinkel, 2004). From this point of view, multi-joint actions present an intrinsic complexity and represent an effective way of studying the central nervous system in a quantitative and experimentally verifiable manner (e.g., Hogan et al., 1987). Complex voluntary movements are characterized by the involvement of the entire body; they require coordination and intentionality and need anticipatory postural adjustments (e.g., Cordo and Gurfinkel, 2004). Just as the output of the movement involving multiple muscles and joints is complex, so is the control exercised by the brain (e.g., Hogan et al., 1987). Many behavioral studies have shown that the complexity of motor response may influence cognitive processes and associated performances. Henry and Rogers (1960) hypothesized that the time to initiate a response increases as the programming process becomes longer and more complex. This hypothesis was confirmed by Christina and Rose (1985) measuring the premotor time (the time from a movement triggering stimulus to the first change in the muscle electrical activity) in three arm actions of increasing complexity, which were produced in response to an acoustic signal. The results showed that, compared to the simplest task, the premotor time became progressively slower for the tasks requiring an increasing number of moving joints. More recently, it has been shown that response time, errors, and movement effectiveness were modulated by movement complexity (simple lifting vs. complex reaching). This effect could be attributed to a top-down strategy aimed at increasing efficiency for the actions most prone to developing kinematic errors (Gálvez-García et al., 2018). In general, when examining the relationship between motor response complexity and cognitive functions, there is a good agreement that the more complex the action, the greater the cerebral load is required (e.g., Floyer-Lea and Matthews, 2004; van der Veer et al., 2024).

At the brain level, neuroimaging studies indicated that premotor and dorsal parietal areas are selectively activated as the complexity of movements increases providing evidence of the participation of these areas in the integration of motor and spatial attributes during the selection of movements (Deiber et al., 1991; Grafton et al., 1992; Wexler et al., 1997; Zimmermann et al., 2012). In addition to this anatomical data, event-related potential (ERP) studies identified the timing of the brain activity associated with movement complexity. Hackley and Miller (1995) demonstrated that the lateralized readiness potential (LRP) enlarged as finger movement complexity increased. The same complexity effect has been shown by Stief et al. (1998) suggesting that complex movements require parallel programming of more effectors. The motor preparation phase indexed by the Bereitschaftspotential (BP) increased as a function of complexity indicating that motor complexity may be encoded in premotor areas (for reviews Shibasaki and Hallett 2006; Di Russo et al., 2017). Also, the contingent negative variation (CNV) amplitude directly depends on movement complexity. Instead, movement complexity seems not to affect CNV in imagined actions, probably because execution requires a greater cognitive complexity than imagination (Kranczioch et al., 2010). A limitation of these studies is that they considered finger movements, without involving other effectors and used self-paced movements. Recently a study of our research group implemented a cognitive visuo-motor discriminative response task (DRT) requiring as a motor response three movements of increasing complexity involving additional body parts (keypress, reaching + keypress, and stepping + reaching + keypress). Results confirmed the modulation of the BP as a function of the complexity in the premotor cortex but, in addition, we also found larger preparatory activity in the parietal and visual areas for the reaching and stepping condition, respectively (Casella et al. 2024). ERP studies investigating the effect of motor complexity on reactive brain processing, i.e., the brain response to stimuli triggering movements of different complexity, are rare. A study comparing ERP obtained in an auditory oddball task between simple (keypress) and more complex (reaching + keypress) responses, found no effects on the studied components N2 and P3 (Lalo et al., 2005). However, (Reiser et al., 2019, 2021) investigated the ERP evoked by an auditory oddball task while the participant had to concurrently complete various outdoor motor tasks. They consistently found, in the late stage of cognitive processing in parietal areas a decrease in the P3 component amplitude for more complex movements. This result was interpreted as a reduction of the available cognitive resources as the motor complexity increases and indicated the key role of attention in cognitive-motor tasks (Reiser et al., 2021). On the other hand, Papin et al. (2024), investigating cognitive-motor interference in naturalistic environments found no P3 effects suggesting that the motor or cognitive skills of participants may affect the outcome with less P3 effect in trained individuals.

Since the literature on brain processing of stimuli requiring increasing motor response complexity is scarce, the following questions remain. If attention plays a key role, can a stimulus triggering motor responses of different complexity affect early visual and attentional processing? The literature on motor complexity provides evidence in support of a cognitive/motor trade-off. Specifically, in tasks requiring a simple motor response, more cognitive and fewer motor resources are deployed, conversely, for complex motor responses, less cognitive and more motor resources are implemented by the brain (e.g., Reiser et al., 2021). The decrease of post-perceptual cognitive processing indexed by the P3 reduction for more complex response movements has been associated with this cognitive/motor trade-off. If this trade-off is real, besides the P3 reduction, we should also find a concurrent amplification of motor-related activity. Indeed, in the literature, this claim is approved as well such as the brain balancing the activation patterns of two mental processes by varying the task's complexity thanks to its feature of incorporation, realigning, or formation of new neural connections (e.g., Lucia et al., 2023). If this trade-off is real, besides the P3 reduction, we should also find a concurrent amplification of motor-related activity.

Considering all the evidence reviewed so far, the present study was aimed at investigating the interaction between the complexity of the motor response in a cognitive task and the brain processing of the stimulus triggering the response. To this aim, we used the same visuo-motor DRT and response modalities used by Casella et al. (2024) since that task evokes large early visual and attentional components such as the P1 and the N1, and large late components such as the P3 (for normative ERP data in that DRT see Di Russo et al., 2019). In addition, the response modality of increasing difficulty used by Casella et al. (2024) was able to produce distinct patterns of preparatory activity indicating the suitability of those response movements.

If the motor response requirements of a DRT interact with early visual processing and attention, we should find modulation of P1 and N1 early ERP components. Moreover, to confirm the existence of a cognitive/motor trade-off, for more complex motor responses we should find a concomitant reduction of the cognitive P3 component and increased brain activity associated with motor processing.

7.2. Methods

7.2.1. Participants

The sample size for this study was determined with the G*power 3.1.9.2 software (Faul et al., 2009). We set the power calculation for a 3 × 2 repeated measures ANOVA design (specified in the statistical analysis section) at 90 % with an $\alpha=0.05$. These computations showed a minimum of 19 participants to reach the effect size of 0.28, taken from the minimum partial eta square of the ERP results of a previous study using a similar experimental ERP design (Mussini et al., 2020). Therefore, 20 volunteers (mean age 23.4 ± 1.4 years, 6 females, 14 males) among the students of the “Foro Italico” University were recruited to participate in the study. Inclusion criteria were the following: absence of chronic somatic problems, absence of any neurological and psychiatric disorders, absence of any medication, and normal or corrected-to-normal vision. All participants were not informed about the aim of the study and were right-handed. Each participant gave his informed consent before participating in this study in accordance with the Declaration of Helsinki after that all procedures were performed in compliance with relevant laws and institutional guidelines and have been approved July 27th, 2023, by the research ethics committee of the University of Rome “Foro Italico” reference number 0146–23.

7.2.2. Stimuli and procedure

The experiment was carried out at the Laboratory of Cognitive and Action Neuroscience, at the University of Rome “Foro Italico”. Participants were tested in a low-lit, sound-attenuated room. They were positioned in front of a computer screen, such that the initial distance between their eyes and the screen was 114 cm. As shown in Fig. 1, the discrimination response task (DRT) was made up of four different visual stimuli, but only two out of four were ‘target’ or ‘Go’ stimuli and the participant had to provide a response (consisting of pressing a key). The other two were ‘non-target’ or ‘No-Go’ stimuli requiring no response. The stimuli consisted of (4 × 4°) square configurations containing horizontal and vertical lines. Each run consists of 80 trials equally divided between target (40) and non-target stimuli (40). Each stimulus has the same probability of presentation ($p = 0.25$). The order of stimuli presentation was randomized both within the single run and between the different runs, to avoid learning effects. The stimulus duration was 250 ms and the inter-stimulus interval varied from 2200 to 3200 ms to prevent stimulus prediction and ERP overlaps with previous and following stimulus. A central fixation point (diameter 0.15 × 0.15°) was always present during the run.

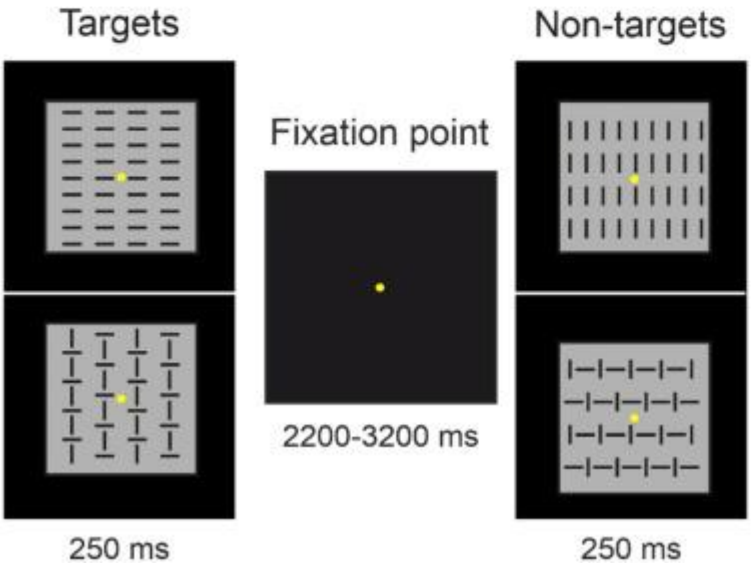


Fig. 1. Representation of the DRT stimuli and timing used in all conditions.

The DRT was performed in the following three different conditions (Fig. 2): In the “Keypress" condition participants were seated on a chair in front of a desk and the response pad was placed on the desk approximately 30 cm away from their body. The participant executed the task with the right index finger already positioned on the response button and they were asked to limit their body movements. They were asked to keep their feet firmly on the ground maintaining a straight posture and avoiding muscle contractions.

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  In the “Reach” condition participants were in the same position as in the “Keypress” condition, but the button was at a greater distance from their body, but such that it could be reached by stretching the right arm. This distance varied according to the length of the participant's arm (50–55 cm). Once the button was pressed, the arm returned to the starting position.
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  In the “Reach-Step” condition participants were standing and the button pad was placed on a 90 cm tall support at a distance such that it could be reached by taking a step forward and simultaneously stretching the right arm. The distance from the keyboard varied according to the participant's arm length and step (75–80 cm). Participants were instructed to always perform the step with the right leg and not to lift the heel of the left foot off the ground.

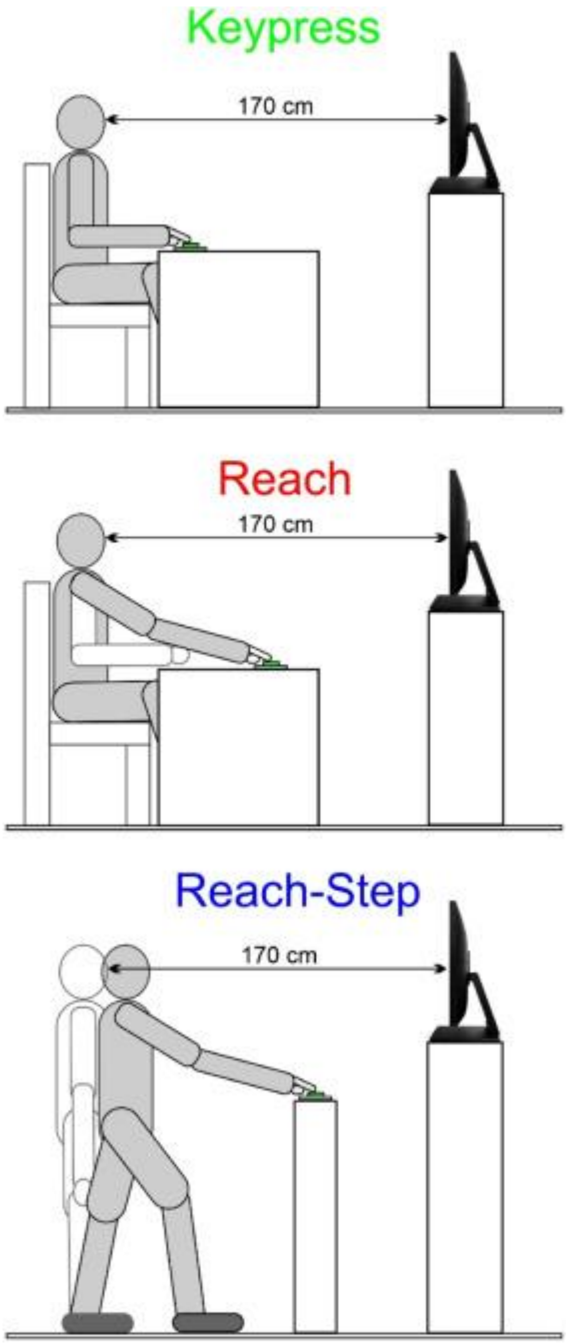

Fig. 2. Representation of response modality in the three conditions.

Each condition consisted of 10 runs and each run contained 20 trials per each of the four stimuli with a total of 800 trials per condition (400 target and 400 for non-target stimuli). The duration of a single run was 3′40’’. In the middle of each condition a 2-minute break was allowed. An additional 5-minute break followed each condition. The duration of each condition was approximately 40′, while the total duration of the experiment was approximately 130′. In all conditions, the response was a keypress made with the right index finger on a response pad. Participants were instructed to respond as quickly as possible, without neglecting accuracy. The condition order was counterbalanced among participants. Before the EEG recording, a minute of warmup (about 20 trials) was allowed to familiarize with the task.

Note that these three experimental conditions and the DRT task were the same as those used in a previous study of this group (Casella et al. 2024) analyzing pre-stimulus ERP components in a distinct set of participants.

7.2.3. Behavioral data

Accuracy and response times in the DRTs were measured. Accuracy was defined as the percentage of errors (i.e., responses not provided to the target stimuli and responses provided to the non-target stimuli) out of the total target and non-target trials delivered. Both speed and accuracy were required to participants, and no time limit was imposed for the response. However, none of the participants had outlier response time or accuracy.

7.2.4. EEG recording and analysis

The participants were tested using a 64-channel EEG system (Brainamp™ amplifiers) with active electrodes (Acticap™) and software (Recorder 1.2 and Analyzer 2.2) all by BrainProducts GmbH (Gilching, Germany). The sintered silver electrodes were mounted according to the 10–10 International System and referenced to M1 and then off-line re-referenced to the M1–M2 average. Horizontal and vertical electrooculograms (EOG) were monitored by bipolar recordings, with electrodes positioned at the left and right external canthi (HEOG) and below and above the left eye (VEOG). The EEG was digitized at 250 Hz, amplified (bandpass of 0.01–60 Hz including a 50 Hz notch filter, 2° order), and stored for offline averaging. The signal was then filtered with 0.1 Hz high-pass and 40 Hz low-pass 2° order filters.

The EEG was segmented in epochs starting 200 ms before the stimulus onset (time 0) and finishing 1700 ms after and processed to reduce ocular artifacts using the propagation factor algorithm available in the Analyzer software. Furthermore, automatic artifact rejection was performed before signal averaging to discard epochs contaminated by signals exceeding the amplitude threshold of ±80 μV, and on average 4.2 % of trials were rejected. The artifact-free trials were averaged, and amplitudes were measured to the −200/0 ms baseline.

To identify the intervals and electrodes to quantify the ERP components, “the “collapsed localizer” method (Luck and Gaspelin, 2017) was used. Based on this method, the three conditions and two trial types (target and non-target) were averaged, and the global field power (GPF) was calculated. The GFP describes the ERP spatial variability considering all scalp electrodes and allowing a reference-independent descriptor of the ERP. The GPF peaks were used to identify the main ERP components and an interval around the peak was used a-priori to establish the interval of analysis of each component. As done in previous studies (e.g., Aydin et al., 2024) an interval based on 80 % of the peak power is reasonably optimal to identify the component range. Using these parameters the following four intervals of analysis were identified: 120–156 ms, 192–224 ms, 412–564 ms, and 690–788 ms. To identify the electrode pool to insert in the analyses, in each of the mentioned intervals, the electrode with the maximum amplitude and the electrode with an amplitude within 80 % of the maximum were included in the pool. According to this procedure, for the first and the second intervals six electrodes were included (PO7, PO8, PO3, PO4, P7, and P8) defining a bilateral "Parieto-Occipital" pool identifiable in the P1 ERP component in the first interval and the N1 in the second. For the third interval, six electrodes were included (CP1, CPz, CP2, P1, Pz, and P2) defining a medial "Centro-Parietal" pool identifiable in the P3 component. For the fourth interval, five electrodes were included (AFz, F1, Fz, F2, and FCz) defining a medial "frontal" pool identifiable such as a frontal late negativity component hereafter defined as N750.

To have an idea of the N750 origin, the source localization of the ERP activity in the 690–788 ms interval was achieved using the "exact low-resolution brain electromagnetic tomography" (eLORETA) software (freely available at www.uzh.ch/keyinst/loreta.htm) to compute the cortical three-dimensional distribution of current density. This method utilizes a discrete, three-dimensional distributed, linear, weighted minimum-norm inverse solution. The weights applied in eLORETA confer precise localization capabilities to test point sources, generating current density images with exact localization, albeit with a limited spatial resolution. Notably, eLORETA demonstrates no localization bias, even in the presence of structured noise, representing an advancement over LORETA and its standardized version, sLORETA (Pascual-Marqui, 2002).

7.2.5. Statistical analysis

After checking for normality and homoscedasticity of the distribution of the variables, the statistical analysis used for the behavioral data (response time and accuracy) was a repeated measure analysis of variance (ANOVA) with the Condition as a 3-level factor (Keypress, Reach, and Reach-Step). For the ERP data, a 3 × 2 repeated measures ANOVA was used for each interval/component. considering the Condition (Keypress, Reach, and Reach-Step) and Trial type (Target and Non-target) as factors. The alpha threshold was set to 0.05. The partial eta squared (η_p^2) was reported as a measure of effect size. To reduce the likelihood of Type 1 errors, the

Bonferroni post hoc test was used to report the corrected p-values. The software used for statistical analysis was Statistica 11 (StatSoft Inc., Tulsa, OK, USA).

7.3. Results

7.3.1. Behavioral data

The ANOVA carried out on the response times showed a significant effect of condition ($F_{(2,38)}$=242,6, $p < 0.001$, η_p^2=0.987). Post-hoc comparisons showed that the Keypress condition response time (535 ms SD=37) was lower ($p < 0.001$) than the other two conditions. The Reach condition response time (970 ms SD=127) was lower ($p < 0.001$) than the Reach-Step condition (1236 ms SD=190).

Regarding accuracy, the ANOVA showed a non-significant effect of condition ($F_{(2,38)} \leq 1$). The error rate was low, being on average 1.7 % (SD=1.6).

7.3.2. ERP data

The ERP waveforms of the three pools of electrodes in the three conditions and for the two trial types are shown in Fig. 3. The scalp topography in the four selected intervals is shown in Fig. 4 for target trials. The earliest component was the P1 peaking at 140 ms and showing a positive bilateral parieto-occipital distribution. The P1 was similar and equally modulated by the condition for both trial types. The N1 peaked at 200 ms and analogously to the P1 showed a bilateral parieto-occipital distribution but of negative polarity. The N1 was comparable for the target and non-target trial types but appeared modulated by condition. The P3 peaked around 480 ms with a positive medial parietal distribution. The P3 was larger for target trials than for non-target trials and was modulated by the condition for target trials only. Finally, a negative late component (N750) peaked around 750 ms over medial frontal areas. The N750 was larger for target trials than for non-target trials and was modulated by the condition for target trials only.

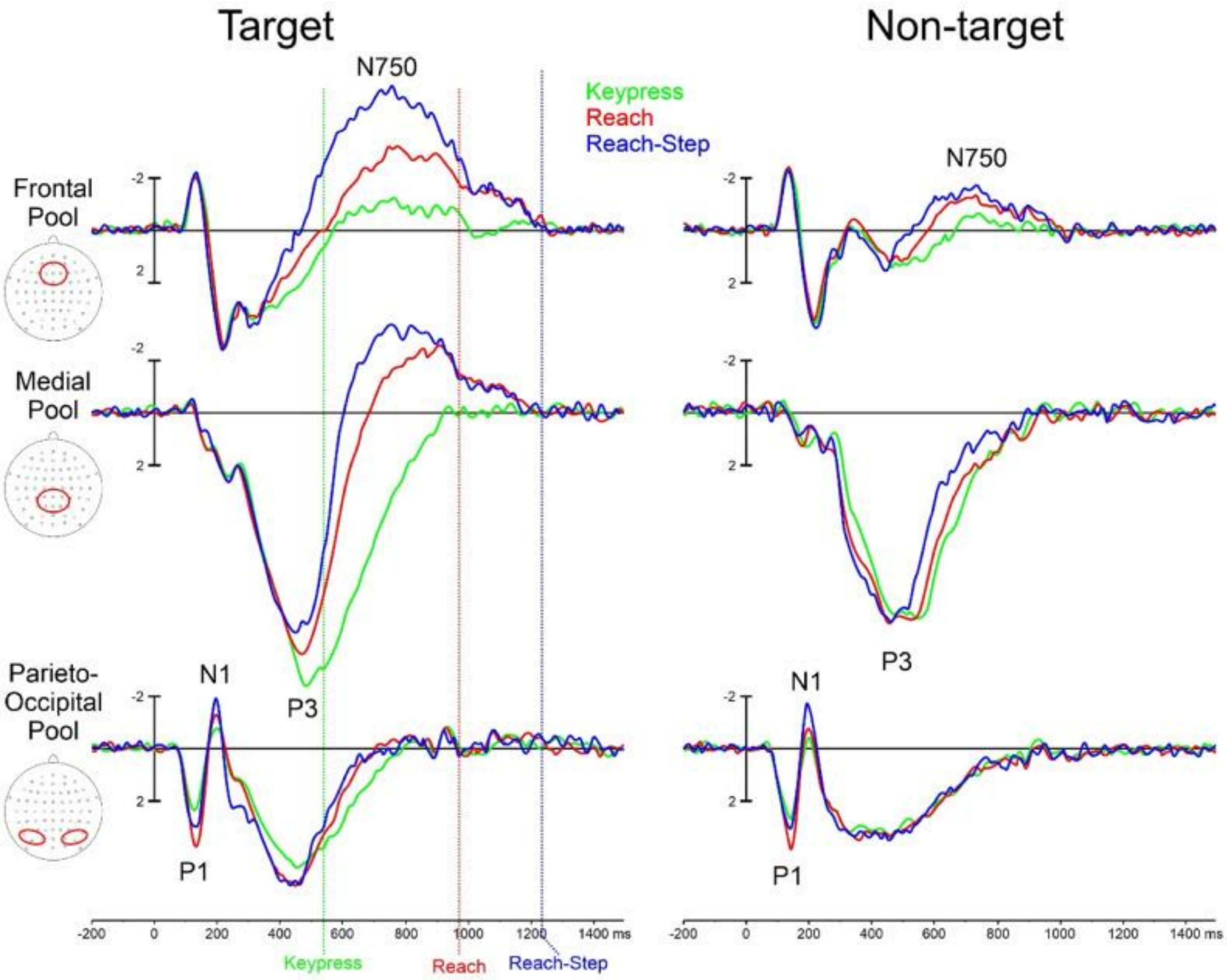

Fig. 3. ERP waveforms in the three conditions. The colored vertical lines indicate the response time. The circles within the head representation indicate the electrodes included in the pool.

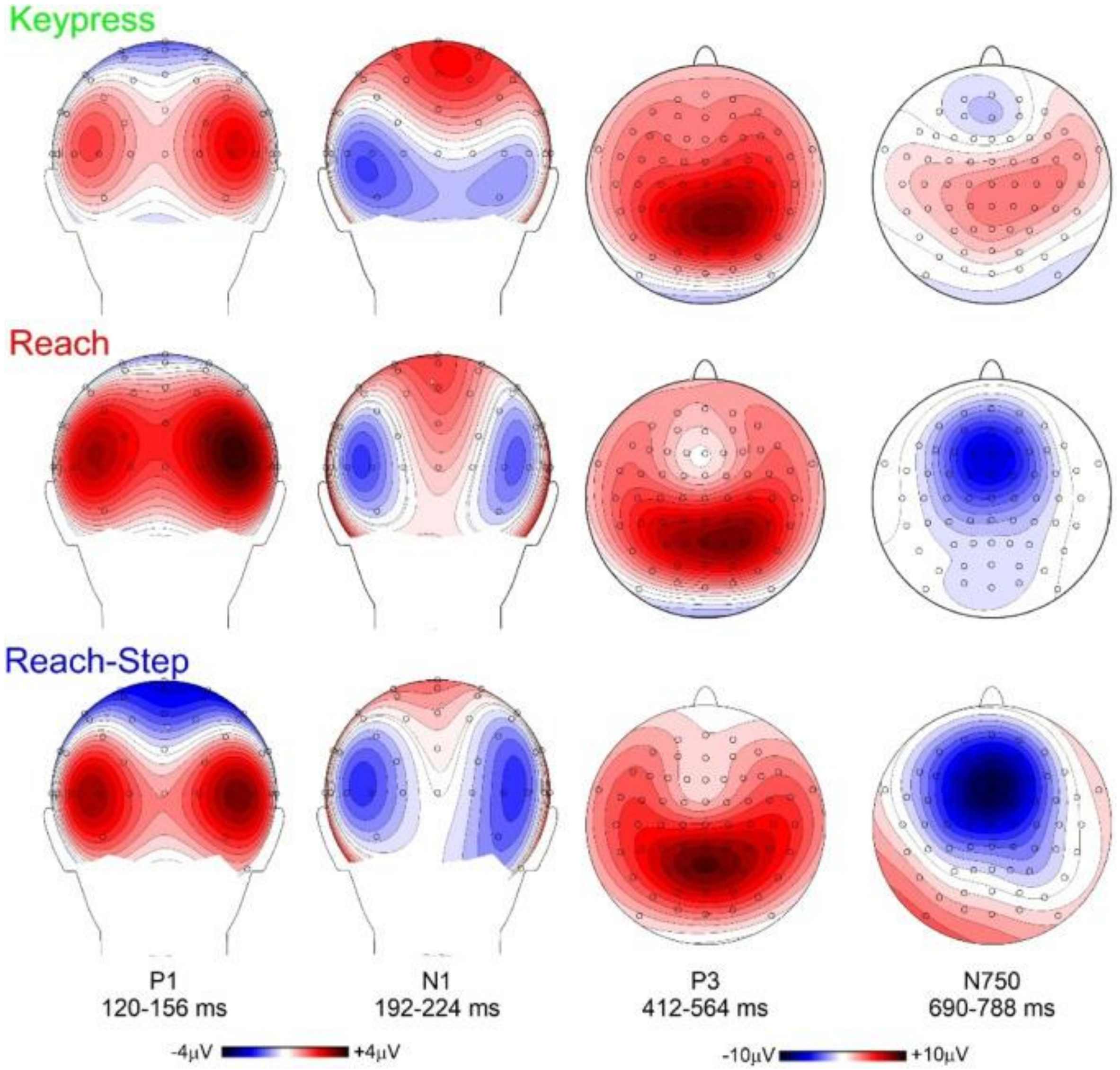

Fig. 4. Scalp topography of the studied components for target trials in the four considered intervals. For the P1 and the N1, a posterior view is displayed, while for the P3 and the N750, a top-flat view is shown.

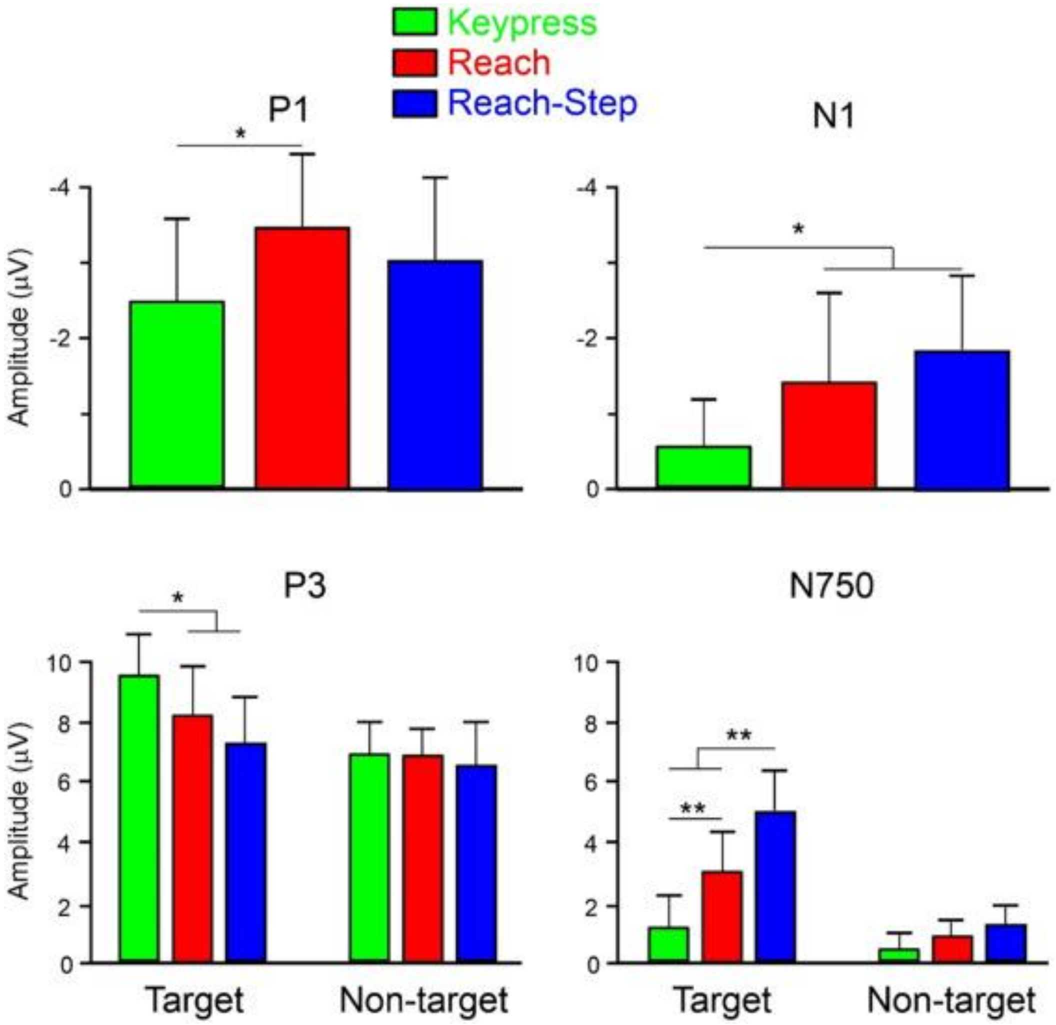

Fig. 5 shows the mean amplitude and variability of the studied components. The ANOVA on the P1 showed a significant effect of the Condition ($F_{(2,38)}$=3.6, p = 0.037, η_p^2=0.158) and post-hoc comparisons indicated that the Reach condition was larger (p = 0.033) than the Keypress condition. The other comparisons were not significant (p > 0.540). The effect of Trial type ($F_{(1,19)}$=3.9, p = 0.085, η_p^2=0.148) and the interaction ($F_{(2,38)}$<1) were not significant.

The ANOVA on the N1 showed a significant effect of the Condition ($F_{(2,38)}$=3.7, p = 0.033, η_p^2=0.164) and the post-hoc comparisons indicated that Reach-Step condition was larger (p = 0.032) than the other two conditions that did not differ each other. The effect of Trial type ($F_{(1,19)}$<1) and the interaction ($F_{(2,38)}$<1) were not significant.
The ANOVA on the P3 showed a significant effect of the Condition ($F_{(2,38)}$=8.7, p < 0.001, η_p^2=0.957) and post-hoc comparisons indicated that in the Keypress condition, the amplitude was larger (p < 0.011) than the other two conditions that did not differ each other. The effect of Trial type ($F_{(1,19)}$=4.7, p = 0.043, η_p^2=0.545) was also significant showing a larger amplitude for

the target trials. However, the interaction was significant ($F_{(2,38)}$=4.1, p = 0.024, η_p^2=0.237). Post-hoc comparisons showed that the significant differences found for the main effect were confirmed for target trials only ($p < 0.05$). For non-target trials, the P3 did not differ among conditions.

The ANOVA on the N750 showed a significant effect of the Condition ($F_{(2,38)}$=4.3, p = 0.020, η_p^2=0.186) and post-hoc comparisons indicated that in the Reach-Step condition, the amplitude was larger ($p < 0.009$) than the other two conditions. In addition, the amplitude of the Reach condition was larger ($p < 0.007$) than the Keypress condition. The effect of Trial type ($F_{(1,19)}$=5.2, p = 0.034, η_p^2=0.215) was also significant showing a larger amplitude for the target trials. The interaction was significant ($F_{(2,38)}$=7.9, p = 0.001, η_p^2=0.302). Post-hoc comparisons indicated that for the target trials in the Reach-step condition, the amplitude was larger ($p < 0.001$) than the other two conditions and that the amplitude of the Reach condition was larger ($p < 0.001$) than the amplitude of the Keypress condition. For the non-target trials, no significant differences were present.

The source localization of the N750 for target trials is presented in Fig. 6. The brain is represented from a frontal view. The activity seems to rise bilaterally from the medial frontal and prefrontal cortex. The contribution of the prefrontal cortex is more evident in the Reach and Reach-Step conditions than in the Keypress condition. The areas more active were the inferior, middle, and superior frontal gyri.

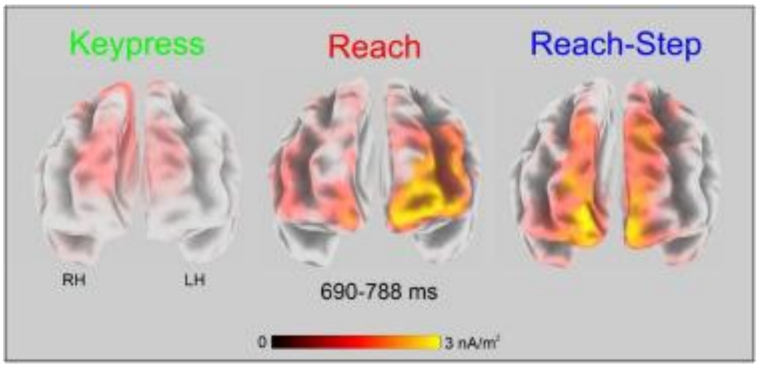

Fig. 6. Source localization of the N750 for target trial in the three conditions and in the 690–788 ms interval (RH=right hemisphere LH=left hemisphere).

7.4. Discussion

Motor responses of different complexity degrees should influence in different ways the brain processes necessary to carry out a cognitive task. However, while we know that performing motor actions using different effectors activate different neural substrates (Heed et al., 2011; Pitzalis et al., 2019), the literature is scarce about the influence of motor responses involving different body parts on a cognitive task. Based on these issues, the objectives of the present study were to verify: 1) if visual and attentional processing depends on motor response complexity; 2) if the balance between cognitive and motor resources employed for the same task is influenced by the motor response complexity.

The behavioral data were as expected since the response time was the longest in the Reach-Step condition, the shortest in the Keypress condition, and intermediate in the Reach condition. This is compatible with the necessary time required to implement the motor response. As motor complexity increases, the duration of the movement itself increases, and therefore the time necessary to carry it out. No effect of the motor response complexity was observed on accuracy. ERP data showed that the P1 amplitude was larger in the Reach condition compared to the Keypress condition. The P1 component is known to reflect the processing of basic stimulus features (e.g., Di Russo and Spinelli, 1999; Zhang and Luck, 2009) and is affected by tasks requiring arm movement towards peripersonal (Eimer et al., 2006; Gherri et al., 2009; Gherri & Eimer, 2011) and personal space (Job et al., 2017). Here, results confirm that stimuli triggering reaching actions may require stronger visual processing than stimuli triggering simple key presses. This is not confirmed by the Reach-Step condition, which even if containing the reach action and being slightly larger than the Keypress condition, did not reach the significance. An explanation for this lack of effect could be that in the Reach-Step condition, the stepping and reaching combination may have reduced the effect.

The N1 was larger in the two more complex tasks compared to the simple keypress. The N1 has been previously associated with early attentional processing (e.g., Di Russo et al., 2019). This result confirms the hypothesis that more complex actions require larger attentional resources. Reaching and stepping responses may require large attentional control likely to take into consideration both the objects' position (the press-button position) and the effectors' position required for the response. The association of the N1 with the attentional controls of objects’ and effectors' positions has been shown in Wascher et al. (2009) and Mason et al. (2015), respectively. They proposed that the N1 would be representative of a dynamic attentional processing system of the surrounding environment aimed at improving the efficiency of the action. From this point of view, compared with the Keypress, the Reach and the Reach-Step conditions require greater coordination of the effectors involved, and greater sensorimotor integration, and therefore seem to require a larger effort in terms of early visual attention. Extending these findings to the results of the present study, it can be deduced that the response motor complexity induces brain adaptations that modulate the mechanisms underlying the attentional orientation towards stimuli triggering motor responses. Considering that the N1 was larger in the two standing positions (Reach and Reach-Step condition) than the sitting position (Keypress), Another data interpretation could be that the N1 was affected by the posture and not the task. However, Bhat et al. (2022) found no differences in any early visual ERP when comparing sitting and standing positions. Overall, since no systematic differences were found among the three conditions, we can safely affirm that the N1 amplitude is modulated by different variables and that the complexity of the action may be one of these.

An alternative, but not exclusive, interpretation of the P1 and the N1 effects could be that they represent a general heightened level of arousal when the movement is more than a keypress.

Results on the P3 showed that in the task with the simplest response motor response modality, the amplitude was larger than in those with a more complex response modality. This result confirms the hypothesis that a lower complexity of the motor response allows greater cognitive resources available. Reiser et al. (2019) reached similar conclusions in an auditory oddball task during the simultaneous execution of motor tasks of increasing difficulty. Reiser and coworkers interpreted the P3 effect as a reduction of the amount of resources available for carrying out the cognitive task during a concurrently complex motor task.

A similar result was obtained by Matthews et al. (2006) comparing ERP evoked by single with dual-task conditions and finding reduction of the P3 evoked by target stimuli in dual task. In addition, neuroimaging studies have also found a reduction in parietal activation during the simultaneous execution of visual/auditory cognitive tasks and motor tasks (Just et al., 2001; Rèmy et al., 2010).

In tasks as the present DRT (or Go/No-go task), the P3 reflects post-perceptual cognitive processes such as decision-making and context updating regarding whether to emit or not the motor response (e.g., Gajewski and Falkenstein, 2013; Smith et al., 2008). The P3 therefore seems to represent the end of a cognitive period, the closure of a perceptual cycle in which certain stimulus features are paid attention regarding the relevance of the stimulus for the task (e.g., Falkenstein et al., 1995; Gajewski and Falkenstein, 2011, Verleger, 1988). Following this literature, in the present study, it can be deduced that in addition to the decision-making, the P3 for target trials, may also reflect a further process linked to motor response complexity.

In addition to the mentioned ERP components that we initially aimed to investigate; we also found another wave over frontal sites. This component had a negative polarity and peaked at about 750 ms and was therefore labeled N750. For target trials, this component was well detectable and was modulated by the motor response. For non-target trials, the N750 was small and independent from the response modality. The N750 seems not connected with response time since the peak latency did not change among conditions even though the relative response time varied consistently. All these features led us to think that this wave could express the motor controls necessary to initiate a complex action. To the best of our knowledge, this component was never reported in Go/No-Go tasks as the present and hardly in other cognitive tasks where the last activity is typically the P3 (see Di Russo et al., 2019 for normative data on this task). However, some studies on brain-computer interface (e.g., Lytaev and Vatamaniuk, 2021) described several minor negative components following the P3 (the N450, N750 and N900) using visual oddball tasks. These waves were smaller than the previous negativity such as the N1 and were prominent over the parieto-occipital areas. These were linked to mechanisms of "exhaustive search" to categorize the incoming information. The topography and the interpretation of these late negativities do not correspond to the present N750. Another component labeled N700 is instead known in the literature but was found in linguistic tasks and has been associated with the retrieval of semantic memories within the prefrontal cortex (e.g., Adorni and Proverbio, 2012; Barber et al., 2013). Therefore, that component could be hardly associated with the N750 found here.

A possible explanation for the lack of data on this late component could be explained by its feature being clearly recognizable for target trials only and in tasks requiring a more complex response modality than a simple keypress. As pointed out in the introduction, there are no studies using those complex response modalities in feature discrimination tasks to study the considered ERP components. Moreover, Bender et al. (2006), studying the timing of post-movement motor processing in simple and alerted reaction time tasks, identified a post-movement negative prefrontal component (negative post-imperative motor variation) that occurred approximately 400–500 ms seconds after key press. However, this component is observable only when the interstimulus interval is sufficiently long and may be associated to the learning of motor sequences. The presence and the modulation of the N750 are in line with the hypothesis we made about the cognitive/motor trade-off of brain functions (e.g., Plummer et al., 2013). According to this view, if the motor demands of a cognitive task increase, fewer cognitive resources are invested by the brain (reduced P3), and more motor resources are instead deployed (larger N750) to correctly execute the action. This phenomenon is also observable in cognitive-motor dual-task paradigms, in which cognitive resources must be distributed across the task (Malcolm et al., 2015; Vasquez et al., 2016). The source localization of the N750 seems to confirm this proposal since the frontal cortex is strongly involved in motor control. Among the various possible trade-off scenarios (e.g., Plummer et al., 2013), the one found here seems to be a motor-priority trade-off since less cognitive resources are used in favoring motor resources.

A possible confounding factor of this study could be that the instruction for the most complex task (Reach-Step) may have increased the cognitive load of participants and affected the result. However, considering that before the EEG recording 20 trials of warmup (about one minute) were allowed to familiarize with the task. We think that it is unlikely that this simple instruction increased the cognitive load since all subjects were right-handed, therefore, the Reach-Step action came naturally to them, in addition, the press button was positioned in the direction of the arm and hand used to respond. These precautions made the execution of the instruction relatively simple and automatic. For a limited number of trials (estimated at 1–2 % of trials), subjects did not comply with the instruction slightly lifting the hill of the left foot. In this case, the instruction was repeated at the end of the run, as many times as necessary lightening the memory load.

Future studies could consider other types of movements and even more complex cognitive and motor tasks to test the limits of motor and cognitive control. Furthermore, the effect of other variables could be evaluated, such as the degrees of freedom allowed by the movement, the hand and leg dominance, the magnitude of environmental distraction, and the level of motor and/or cognitive expertise since Papin et al. (2024) indicate that these factors may affect brain processing during cognitive/motor task.

7. Conclusions

In this study, three motor responses of increasing complexity to the same cognitive task were compared. We observed that if the response modality is more complex than just a button press and requires additional reaching and stepping movements, the brain resources used for the motor and the cognitive task vary as a function of motor complexity. In particular, late cognitive processes in parietal areas indexed by the P3 were suppressed for stimuli requiring complex actions. However, as in a motor-priority cognitive/motor trade-off system, activity rising from motor-related brain areas progressively increased probably to reinforce the motor control over the initiated action.

8. Chapter. Effects of walking on anticipatory brain processing during a concurrent cognitive task

8.1. Introduction

Body movement and cognition are strongly interconnected as demonstrated by multiple overlaps in the brain structures and networks underlying these functions. It has been hypothesized that, in humans, these functions share a common evolutionary history (Llinas., 2002; Mendoza et al., 2014; Leisman et al., 2016), in particular, bipedalism played a key role in promoting brain development (Harcourt-Smith, 2010). The movement of one's own body (ego-motion) and in particular walking, is an exceptionally complex process that requires the integration of mainly visual and other sensory signals from internal and surrounding environments (for a review, see Greenlee et al. 2016). It has been widely demonstrated that walking is influenced and largely controlled by the optic flow, also known as the flow field, which is the apparent motion of the visual field that occurs as a result of ego-motion (e.g., Warren et al., 2001; Lamontagne et al., 2007; Bruggeman et al., 2007; Salinas et al., 2017). Individuals use information deriving from the flow field to gather visual cues essential for guiding their walking and to interpret somatosensory information. As a result, people unconsciously adjust their gait to synchronize with the features of the optic flow (e.g., Konczak, 1994; Salinas et al., 2017) and to calibrate the biomechanical aspects of walking based on visual information (Mohler et al., 2007).

Optic flow can be easily simulated on computer monitors, contributing to the success of video games and virtual reality experiences. At the scientific level, simulated flow fields have been extensively used to explore the behavioral and neural basis of motor and cognitive control during walking. Several studies have demonstrated the interaction between optic flow, cognitive and motor processes; for instance, forward optic flow has priority in perceptual awareness, regardless of walking direction and proprioceptive abilities, as if our visual system were finely tuned to the optic flow patterns encountered in daily life (e.g., Durgin et al., 2007; Motyka et al., 2021). This interaction is also supported by neuroimaging studies which have identified a network of sensory and associative brain areas that respond to both leg movements and simulated flow fields. These findings indicate the existence of a complex brain network underlying locomotion (e.g., Di Marco et al., 2021; Pitzalis et al., 2019; Serra et al., 2019). Therefore, far from being a completely automatic action, as long believed, walking requires significant interactions between motor and cognitive processes. Indeed any neurodegenerative diseases affecting cognitive functions consistently involve motor disorders, and, in particular, locomotion. Even healthy individuals unconsciously adjust their walking parameters, such as speed and direction, when they need to adapt to changing conditions or simultaneously engage in other tasks that require the same cognitive resources (Yogev-Seligmann et al., 2008).

To study the relationship between cognition and ego-motion, cognitive-motor dual-tasks (CMDT) can be employed. A dual-task involves the execution of two independent tasks simultaneously, each with distinctive objectives and measurable parameters (e.g., McIsaac et al., 2015). The dual-task effect is defined as the change in performance that can be observed in one (usually the primary task) or both tasks when they are performed simultaneously, compared to when they are performed separately. According to the capacity-sharing theory (e.g., Abernethy 1988), this change is typically detrimental, as it reduces the cognitive and motor resources available for each task, necessitating their distribution between the two. Similarly, the bottleneck theory (e.g., Malcolm et al., 2015; Vasquez et al., 2016) posits that when two tasks are processed by the same neural network, a bottleneck occurs in information processing. As a consequence, the second task will be delayed until the first task is completed. Other models of the dual-task effect, such as the multiple resources and crosstalk theories (e.g., Bayot et al., 2018; Pashler, 1994; Yogev-Seligmann et al., 2008), suggest that two simultaneous tasks may not interfere with each other if they involve similar sensory inputs and neural populations. In such cases, a performance improvement may occur if one of the two tasks plays a facilitating role. This facilitation has been associated with over-additive activation of the brain areas involved in the task and in the prefrontal and parietal areas, which play a key role in coordinating the simultaneous execution of multiple tasks (for a review see Leone et al., 2017).

The literature on CMDT involving walking as the motor task has found contrasting results. Some studies observed a decline in attentional performance, while others reported detriments in the motor performance or even facilitation (e.g., Leone et al., 2017; Yogev-Seligmann et al., 2008). More recently, Patelaky et al. (2023) found enhancements in response speed and accuracy on a cognitive Go/No-go task in over half of the participants while they walked on a treadmill. Using event-related potentials (ERP) measures, this study found a reduction in the cognitive N2 and P3 components during walking. Similarly, De Sanctis et al. (2014) found no behavioral effect of walking during a Go/No-go task but observed a reduction in the N2 and P3 components. These results were attributed to a flexible reallocation of cognitive resources that can be adaptively recalibrated while walking, using a controlled processing mode that optimizes cognitive performance. A limitation of these studies is that they only considered reactive brain processing (activity following an event), neglecting the preparatory brain activity that precedes the event. In addition, comparisons were made between sitting in a chair and walking on a treadmill; therefore, they did not control for the variability due to different body positions. Finally, the absence of a simulated flow field while walking on the treadmill made the task less ecologically valid.

To study preparatory brain activity, the ERP method is the technique of choice (e.g., Russo et al., 2019). This method can measure the cortical temporal dynamics occurring before the appearance of stimuli that require cognitive processing. Additionally, it is not limited by movements such as walking. Therefore, compared to other techniques, ERP does not impose excessive limitations or restrictions regarding the type and extent of movements, thereby preserving the ecological nature of the actions as much as possible.

Regarding the preparation phase before stimulus onset, the most well-known ERP component is the Bereitschaftspotential (BP) (for reviews, see Di Russo et al., 2017; Shibasaki & Hallett, 2006). The BP is a negative component that begins 1-3 seconds before the onset of a stimulus or the initiation of a movement - depending on whether the movement is externally triggered or self-paced. It progressively increases in amplitude and reaches its peak at the stimulus or movement onset. The BP reflects the motor preparation for the upcoming action, is topographically focused over the central-medial scalp, and has been localized in the supplementary motor area (SMA) (e.g., Di Russo et al., 2017; Shibasaki & Hallett, 2006). In discrimination response tasks (DRT), larger BP amplitude has been associated with faster response speed (e.g., Di Russo et al., 2019). In addition to BP, in DRTs as the Go/No-go task, is possible to record other preparatory components (for a review, see Di Russo et al., 2017), such as prefrontal negativity (pN), localized in the prefrontal areas and associated with higher cognitive functions such as top-down attentional and inhibitory control. Larger pN amplitude has been associated with higher response accuracy (e.g., Berchicci et al., 2020; Bianco et al., 2020; Di Russo et al., 2019).

Given the inconsistencies in the cognitive-motor dual-task literature, the objective of the present study was to examine whether walking affects behavioral performance while performing a cognitive task, and in particular, anticipatory brain processing. In addition, we aimed to test the effect of a naturalistic walking situation using a simulated flow field to reproduce a realistic walking experience, even when using a treadmill. Finally, unlike previous studies, we used a more straightforward comparison by contrasting walking with a standing condition. To achieve these aims, we measured the BP and pN anticipatory ERP components during a DRT executed during walking and standing conditions, while also modulating the presence or absence of a flow field that was coherent with the walk.

According to the literature, if brain resources for cognitive tasks are redistributed to motor control during walking, we expect to observe a decline in behavioral performance, as posited by the capacity-sharing and bottleneck theories, along with a reduction in both BP and the pN components. Conversely, if the brain can recalibrate its functions while walking to optimize cognitive performance (e.g., De Sanctis et al., 2014), we would expect no difference in performance during walking. On the other hand, if the brain efficiently manages dual tasks by optimizing cortical integration and enhancing cognitive resources (as suggested by the multiple resources theory), we should observe improved behavioral performance and larger BP and pN amplitude in walking compared to the standing condition. Furthermore, the presence of a coherent flow field that reproduces a more naturalistic setting is expected to enhance the effect of walking.

8.2. Methods

8.2.1. Participants

The sample size was calculated based on a power analysis conducted using G*Power software (version 3.1.9.4). The parameters were set for a within-between analysis of variance (ANOVA) with the alpha level (α) of 0.05, a statistical power of 0.95, and an effect size (f(V)) of 0.67. The effect size was calculated from the average partial eta squared (η_p^2) reported in a previous study employing a similar analysis (Lucia et al., 2024). These settings estimated a sample size of 40. A total of 40 volunteers were then recruited from the student body of the University of Rome "Foro Italico". The sample included 21 males and 19 females, with ages ranging from 20 to 36 years (mean age=24.1 years, SD=3.2).

The following exclusion criteria were applied: 1) the presence of neurocognitive or motor disorders that could impair the understanding of the instructions and execution of the task; 2) severe vision problems that could hinder stimuli discrimination (participants with minor vision issues that could be corrected were included).

All participants provided informed consent for the study and were naïve to the purpose of the experiments. The work was conducted in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki, 1964), and it was authorized by the university's ethics committee.

8.2.2. Procedure

Participants were pseudo-randomly assigned to two groups of 20, balanced for sex and age, to minimize learning effects associated with the repetition of the same task. In the same session, all participants performed a visuomotor discrimination response task (DRT) under two conditions: 1) while walking on a treadmill (Walk condition), and 2) while standing still on a treadmill (Still condition). The order of the two conditions was counterbalanced among participants to control the effects of learning and physical activity.

The DRT was administered using a 32-inch monitor positioned 114 cm from the participant's eyes, providing a visual field subtending 35.4 × 31.7 degrees of visual field. The monitor displayed a steady fixation point in the center, which subtended 0.15 × 0.15 degrees. Participants were instructed to pay attention to the stimuli appearing on the screen and to respond by pressing a button as quickly and accurately as possible when two target stimuli were displayed, while refraining from responding when two non-target stimuli appeared (Go/No-go task).

As shown in Figure 1, each stimulus consisted of a 4 × 4 degrees grey square composed of a 36 black segments pattern. The two target stimuli contained, horizontal segments and columns of vertical and horizontal segments; the two non-target stimuli displayed vertical segments and lines of vertical and horizontal segments. In other words, the non-target stimuli were 90° rotated to the left with respect to the target stimuli.

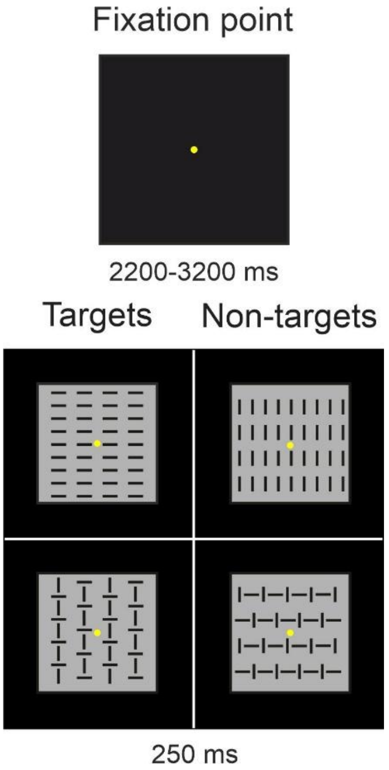

Figure 1: **Schematic illustration of stimuli used in the DRT.**

To test the effect of realistic walking, one group (the Flow field group) viewed a continuous video, during the DRT, featuring dots expanding radially and centrifugally to represent a flow field coherent with a walking speed of 1 km/h, which was the target speed in the Walk condition. The other group (No Flow field group) performed the task in front of a black background, as shown in Figure 2.

Participants used a motorized treadmill (ISE®, model SY-1006) set to a speed of 1 km/h, with the keypress device held in their right hand and activated using the right index finger. The experiment was carried out in a low-lit, sound-attenuated room.

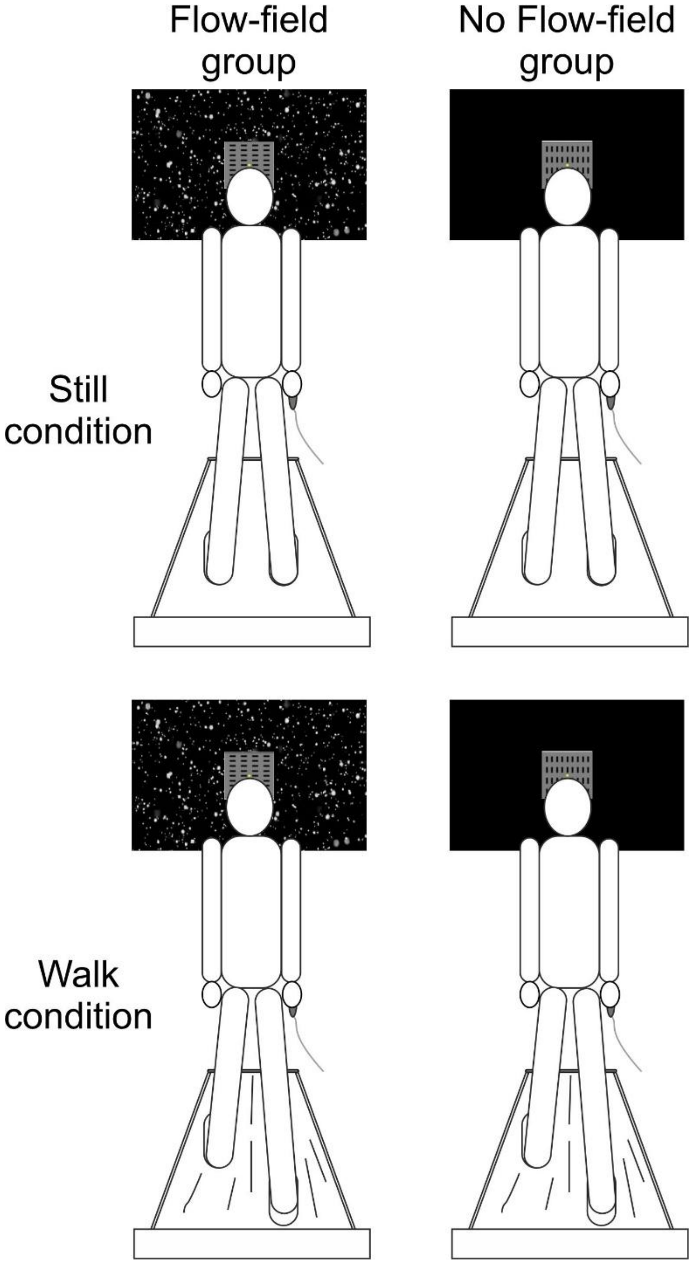

Figure 2. Schematic illustration of experimental conditions. Representation of the two backgrounds used in the study, with and without the flow field video. The size and speed of the dots varied in logarithmic progression, creating an illusion of movement. In the Still condition, participants remained steady, while in the Walk condition, they walked at a speed of 1 k/h.

The DRT stimuli were presented for 250 ms in rapid succession, with a variable inter-stimulus interval ranging from 2200 to 3200 ms. Each run consisted of 40 target stimuli and 40 non-target stimuli presented in random order, resulting in a target probability of 50%. The duration of each run was approximately 3 minutes. For each condition, 10 runs were completed, with breaks in between, with a total duration of about 75 minutes.

8.2.3. Behavioral data

In the DRT, two parameters of behavioral performance were assessed: response time (RT), defined as the average time to respond to target stimuli, and percentage of errors (Err%), which serves as an accuracy index. Err% was calculated by summing false alarms (responses to non-target stimuli) and omissions (missed responses to target stimuli).

8.2.4. EEG recording and analysis

Before the task, an EEG cap with 64 active scalp electrodes (Acticap$^{\text{TM}}$) was mounted according to the international 10-10 system. During the task, participants underwent EEG recording using two Brainamp$^{\text{TM}}$ amplifiers and the Recorder 1.2 software. The EEG data were processed offline with Analyzer 2.2 software, all provided by BrainProducts GmbH (Gilching, Germany). The electrodes were referenced to the averaged mastoids. Eye movements were monitored with an additional Brainamp$^{\text{TM}}$ amplifier and two pairs of bipolar electrodes: one pair was positioned on the external canthi of the eyes to monitor the horizontal movements, while the other pair was used placed above and below the left eye to monitor vertical movements.

The EEG data were digitized at a sampling rate of 250 Hz and band-pass filtered using a Butterworth zero-phase filter (0.01–80 Hz) along with a 50 Hz notch filter (second order). The signal was then offline filtered with 0.1 Hz high-pass and 30 Hz low-pass filter. Blink and other eye movement artifacts were automatically corrected using the Gratton diffusion algorithm implemented in Analyzer 2.2. The EEG data were segmented in 1400 ms windows, spanning from 1100 ms before stimulus onset to 300 ms after the onset. Semi-automatic artifact rejection was carried out before signal averaging to discard epochs exceeding an amplitude threshold of ±80 µV. Both target and non-target trials were considered. The artifact-free trials were averaged, and pre-stimulus activities were measured against a baseline of -1100 to -900 ms.

To select the electrodes and intervals for statistical analysis, the “collapsed localizer” method was employed (Luck & Gaspelin, 2017).The average across all groups and conditions was calculated, followed by the computation of global field power (GFP) to identify the analysis interval. The interval during which the GPF exceeded 70% of its maximum value (from -280 to 0 ms) was selected for further analysis. This cutoff was considered reasonable for pre-stimulus ERPs and has been utilized in several previous studies (e.g., Mussini and Di Russo 2023). Similarly, electrodes exhibiting amplitudes greater than 70% of the maximum value in that interval were aggregated into spatial pools for statistical purposes. Two distinct pools of activity were identified: a prefrontal pool composed of Fp1, Fpz, Fp2, AF7, AF3, AFz, AF4, and AF8 (representing the pN component), and a central pool including C1, Cz, C2, CP1, CPz, CP2, P1, Pz, and P2 electrodes (representing the BP component).

8.2.5. Statistical analysis

First, the normality and homoscedasticity of the population regarding the measured variables were verified. Each measure was then submitted to a 2×2 mixed analysis of variance (ANOVA) with the within factor Locomotion at two levels (Still vs. Walk), and a between factor Flow field at two levels (Flow field vs. No Flow field).

The alpha level was set to 0.05. The partial eta squared (η_p^2) was reported as a measure of effect size. All statistical analyses were carried out using Statistica 11 software (StatSoft Inc., Tulsa, OK, USA).

8.3. Results

8.3.1. Behavioral data

Behavioral results are shown in Figure 3. The ANOVA on RTs showed a significant effect of the Locomotion factor ($F_{(1,38)}=51.4$, $p<0.001$, $\eta_p^2=0.575$), indicating shorter RTs for the Walk condition (445 ms ±37) compared to the Still condition (463 ms ±39). The significant effect of the Flow field factor was also observed ($F_{(1,38)}=4.2$, $p=0.047$, $\eta_p^2=0.099$), indicating shorter RTs for the Flow field condition (442 ms ±31) compared to the No Flow field (465 ms ±40) condition. The interaction between these two factors was not significant ($F<1$).

The ANOVA on the Err% showed a significant effect of the Locomotion factor ($F_{(1,38)}=5.4$, $p=0.025$, $\eta_p^2=0.124$), indicating lower error rates for the Walk condition (4.1% ±1.6) compared to the the Still condition (5.2% ±1.8). The Flow field factor also showed a significant effect

($F_{(1,38)}=8.4$, $p=0.006$, $\eta_p{}^2=0.181$), indicating lower errors for the No Flow field (3.2 ms ±0.9) compared to the Flow field (6.2% ±2.2) condition. The interaction between these two factors was not significant ($F<1$).

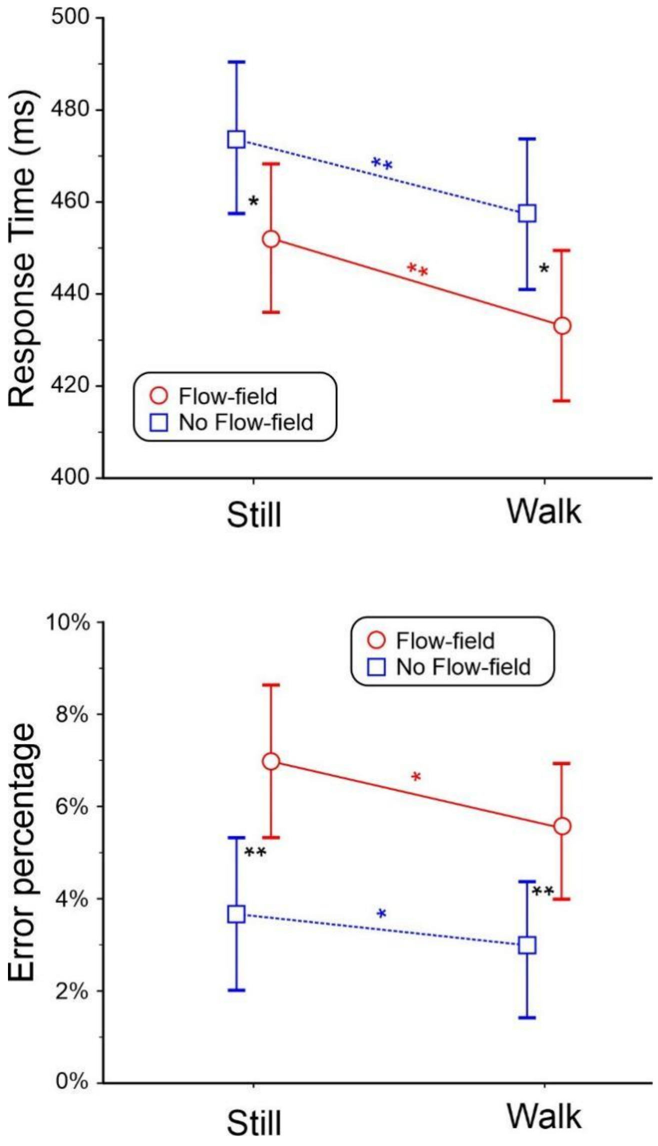

Figure 3: **Mean response time and error percentage in the studied conditions**. Vertical lines denote the 0.95% confidence interval. *p<.05 **p<.001

8.3.2. ERP data

Figure 4a shows the ERP waveforms for the four conditions at the prefrontal and parietal pools of electrodes associated with the pN and BP components, respectively. The waveforms show the typical slow negative ramp of the preparatory ERP, detectable starting approximately 800 ms before the stimulus onset and peaking at the moment of the stimulus arrival. Figure 4b illustrates the scalp topography from -280 to 0 ms, showing a predominant focus on medial centroparietal areas (the BP component) and, to a lesser extent, on frontal and prefrontal areas (the pN component).

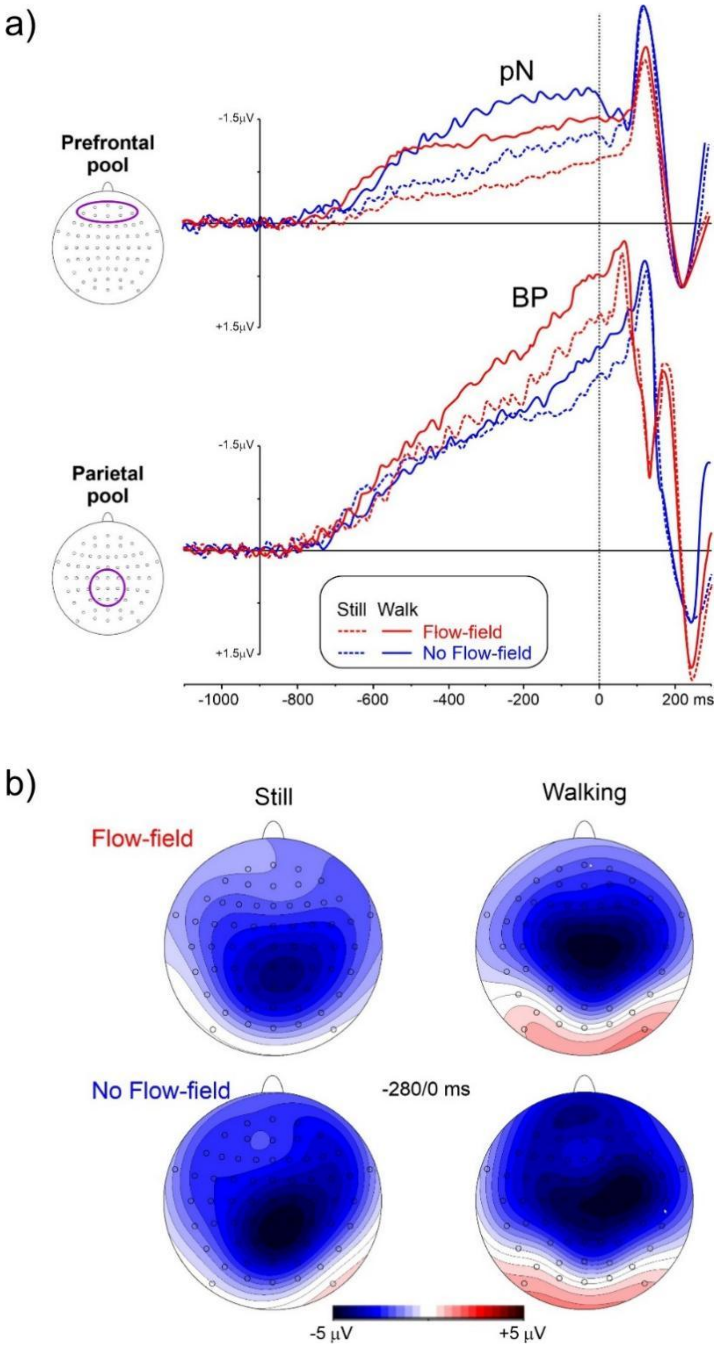

Figure 4: **a) ERP waveforms in the four conditions at the prefrontal and the parietal pool. b) Scalp topography (top-flat view) in the -280/0 ms intervals.**

The ANOVA on the pN component indicated a main effect of Locomotion ($F_{(1,38)}=12.3$, $p=0.001$, $\eta_p^2=0.245$), revealing a larger amplitude for the Walk condition (1.59 □V ±0.36) compared to the Still condition (-1.42 □V ±0.29) condition. The Flow field factor also showed significant effects ($F_{(1,38)}=19.2$, $p<0.001$, $\eta_p^2=0.336$), indicating a larger amplitude for the No Flow field (-1.84 □V ±0.38) than for the Flow field condition (-1.18 □V ±0.25). The interaction between these two factors was not significant ($F_{(1,38)}=1.1$, $p=0.294$). Figure 5a displays the mean pN amplitude across all conditions.

The ANOVA on the BP component indicated a main effect of Locomotion ($F_{(1,38)}=4.8$, $p=0.034$, $\eta_p^2=0.113$), showing a larger amplitude for the Walk condition (3.37 □V ±0.67) compared to the Still condition (-2.84 □V ±0.42). The Flow field factor also exhibited a significant effect ($F_{(1,38)}=21.9$, $p<0.001$, $\eta_p^2=0.366$), indicating a larger amplitude for the Flow field condition (-3.91 □V ±0.69) compared to the No Flow field condition (-2.28 □V ±0.46). The interaction between these two factors was not significant ($F_{(1,38)}=1.3$, $p=0.268$). Figure 5b shows the mean BP amplitude across all conditions.

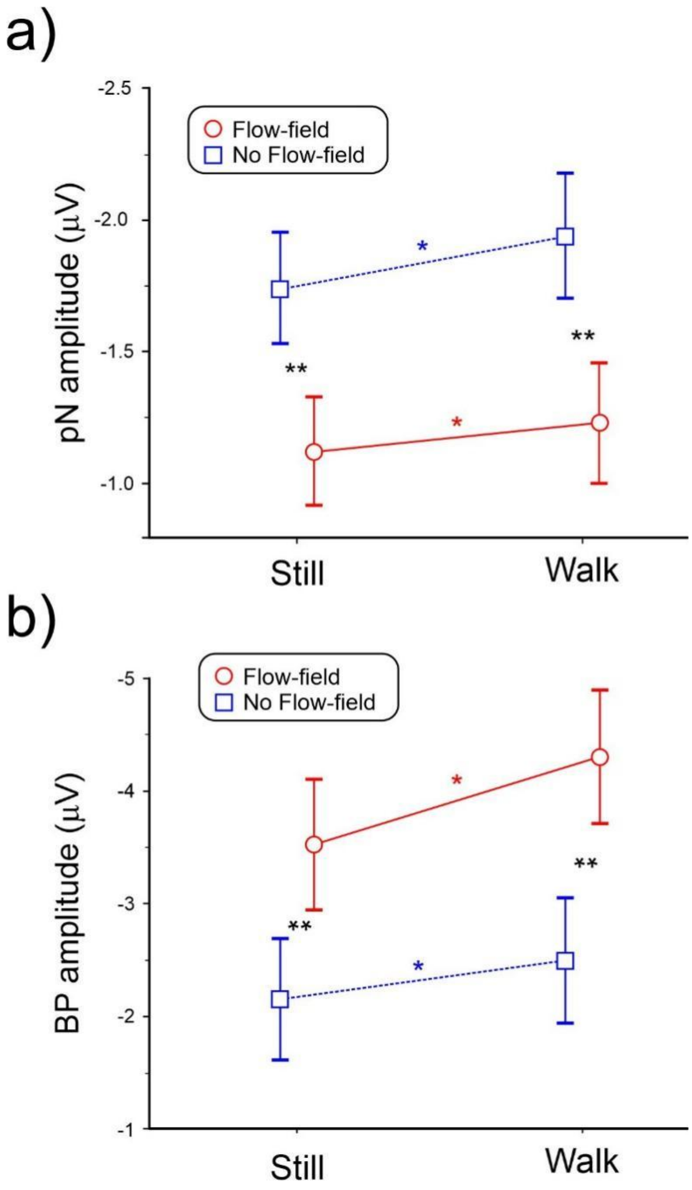

Figure 5. Mean amplitudes in all conditions for the pN (a) and the BP (b) components. The vertical bars indicate 0.95 confidence intervals. *p<.05 **p<.001

8.4. Discussion

The present work aimed to investigate the effect of cognitive-motor dual tasks (CMDT) on behavioral performance and anticipatory brain processes. Specifically, we sought to determine whether performing a visual discrimination response task while walking might lead to improvements - consistent with the multiple resources theory - or worsening - according to the capacity sharing and bottleneck theories - in response speed and accuracy. Additionally, we aimed to associate these potential behavioral changes with modulations in the amplitude of the motor (BP) and cognitive (pN) preparatory ERP components. Finally, we examined whether a simulated optic flow, congruent with the walking direction, could amplify or reduce the effect of walking on anticipatory brain processing and behavior.

Behavioral results indicated that locomotion improved both RTs and accuracy, supporting findings from previous dual-task studies (e.g., Brisswalter et al., 1995; Yagi et al., 1999; Collardeau et al., 2001; Mc Morris et al., 2003; Davranche et al., 2004; Davranche et al., 2006; Audiffren et al., 2008; Tomporowski & Audiffren, 2014). For example, Collardeu et al. (2001) found RTs improved in a simple detection task during treadmill walking compared to a stationary condition, both before and after the exercise. They attributed this enhancement to the increased arousal induced by physical exercise. Similarly, Yagi et al. (1999) reported comparable results in a dual-task paradigm, combining simple aerobic exercise with visual and auditory discrimination tasks. Audiffren et al. (2008) also found that pedaling reduced the RTs to auditory stimuli, suggesting that ongoing exercise activates motor processes. Davranche et al. (2004, 2006) emphasized that exercise influences motor and premotor RTs differently; in simple detection tasks, only motor RTs were modulated by concurrent physical activity, while in choice tasks, both motor and premotor RTs were reduced, as physical movement interacts with the perceived visual stimulus intensity, facilitating processing.

The aforementioned literature and the present findings suggest that behavioral performance in cognitive tasks may be enhanced by concomitant low-intensity physical activity, such as slow walking on a treadmill. This walking modality, which poses no obstacles, is a relatively automatic process that may increase cognitive function, without overloading it. Thus, this level of physical activity not only did not interfere with concurrent cognitive tasks but may also benefit the recruitment of additional cognitive resources, leading to improved task performance. This conclusion is consistent with the meta-analysis of Chang et al. (2012), which indicates that physiological changes induced by exercise have beneficial effects on cognitive processes and, consequently, on behavior.

At the neural level, we found that the BP (associated with motor preparation for the DRT) was strengthened by locomotion. This result can explain the faster RTs observed behaviorally and indicates that anticipatory motor resources may be facilitated by walking. An increase in DRT-related BP during walking may suggest that preparing for an upper-limb action while walking allows additive activity of the SMA. This phenomenon may occur because heightened arousal induced by the dual task could enhance brain activity and therefore performance (McMorris and Graydon, 2000; Schaefer et al., 2010), likely because the two tasks do not overload the cognitive capacity or interfere with one other (e.g., Yogev-Seligmann et al., 2008).

A similar rationale applies to the pN effects as well. This component is thought to reflect cognitive anticipation, intended as top-down attentional control and inhibition in prefrontal areas (e.g., Di Russo et al., 2016; 2017). The increased pN during walking may be an index of improved proactive cognitive control, which explains the improvement in response accuracy observed during walking. The modulatory effect of movement on this component has been previously demonstrated by Berchicci et al. (2013), who associated it with the degree of top-down control and prefrontal cortex activation (Berchicci et al., 2013, 2014). Furthermore, the prefrontal cortex benefits from the increased activation of the noradrenergic and serotonergic systems induced by moderate physical activity (e.g., McMorris, 2016).

Compared to standing, greater activation of prefrontal and premotor areas suggests improved signal-to-noise ratio and, ultimately, enhancements in cognitive system efficiency (McMorris & Hale, 2015; McMorris, 2016). Since physical activity as deambulation enhances arousal, and in addition walking slowly on a treadmill (and in general without obstacles) is characterized by a high degree of familiarity and a low degree of complexity (e.g., Nutt et al., 1993; McIsaac et al., 2015), it may facilitate cognitive performance producing additive brain activity in prefrontal and premotor brain areas. Animal studies have similarly shown that acute and moderate physical exercise increases catecholamine release, which enhances prefrontal cortex activation while positively affecting signal detection in the sensory areas, thereby facilitating perception and attention to the concurrent task.

Regarding the effect of the simulated flow field, we found that it improved RTs but decreased accuracy in the cognitive task. The RT improvement, linked to increased motor preparation, may stem from an individual’s tendency to synchronize their walking with the optical flow, therefore reducing the motor load of walking. A substantial body of literature supports the idea that individuals unconsciously use visual information from optic flow to regulate their gait (e.g., Konczak, 1994; Mohler et al., 2007; Salinas et al., 2017). In the present study, walking parameters were fixed and predetermined, suggesting that synchronization with the optic flow could facilitate motor preparation and speed of response. Conversely, the reduction in accuracy (associated with decreased cognitive preparation) likely arises from the increased amount of visual information that interferes with the visual cognitive task. According to the multiple resources model (e.g., Yogev-Seligmann et al. 2008), dual tasks improve performance in one or both tasks unless the cognitive demands are excessive, or the two tasks compete for the same sensory resource or body part. With the addition of optic flow, cognitive demands increased, likely drawing visual and/or attentional resources away from the cognitive task. As Bock (2008) demonstrated, the demands of visual processing critically influence task complexity and the resulting interference between concurrent tasks. During walking, in the absence of optic flow and ego-motion-related visual information, individuals may adapt their locomotion control and allocate their free cognitive resources more effectively to enhance task performance (Seno et al., 2015). Furthermore, Wickens (2002), in interpreting the experimental discrepancies relating to intra-modal advantages/disadvantages phenomena in the light of the theory of multiple resources, hypothesized that two competing visual channels always result in an additional cost. This is determined by the need to divide attentional resources when the two elements to be processed are distant, by the confounding effect caused by the overlap and masking of one on the other, when they are temporally and spatially close (e.g., Bock, 2008; Herath et al., 2001; Wickens, 2002).

In conclusion, locomotion seems to enhance both motor and cognitive preparation, as indicated by the BP and the pN ERP components, resulting in improvements in response time and accuracy. The introduction of optic flow generated a similar increase in motor preparation and response times but was associated with reduced cognitive preparation, leading to decreased accuracy. The multiple resources theory can explain these results: performing a cognitive task that requires upper limb responses during easy walking does not generate interference; indeed, walking can facilitate the cognitive tasks by increasing preparatory activity in the prefrontal and premotor areas. The simulated optical flow, by inducing the illusion of movement, further activates pre-motor resources and facilitates response times. However, this additional visual input increases the cognitive load, potentially drawing anticipatory cognitive resources (primarily attentional and inhibitory) away from the prefrontal areas and resulting in reduced response accuracy.

From an applicative perspective, walking while performing a visuomotor cognitive task could benefit cognitive-motor dual-task training protocols, as it may lead to heightened activity in anticipatory brain processes within prefrontal and premotor areas, thereby improving behavioral performance. Using a simulated flow field may further improve response speed but could reduce accuracy; therefore, it is advisable to employ the flow field stimulation only in reaction training protocols.

Future studies could consider a more specific analysis of walking by applying gait analysis devices to the treadmill combining different speeds to simulate different real-world actions. This could be useful in situational sports, where the athlete quickly switches from a slow to a faster dual-task situation, where physical and cognitive effort increases.

9. The role of optic flow on reactive brain processing in cognitive tasks during locomotion

9.1. Introduction

Motor and cognitive brain processes are mutually interconnected and influence each other. It has been proposed that they evolved in parallel, sharing the same underlying brain circuits (e.g., Llinás & Ribary, 2001; Mendoza & Merchant, 2014; Leisman et al., 2016) and that brain development was promoted by bipedalism (Harcourt-Smith, 2010). Locomotion is an emergent behavior that depends on the efficient integration of multisensory information (e.g., Greenlee et al., 2016), but it is primarily controlled by the visual perception of the optic flow (e.g., Warren et al., 2001; Lamontagne et al., 2007; Bruggeman et al., 2007; Salinas et al., 2017).

Role of optic flow in locomotion

Optic flow is defined as the visual shifts occurring on the retina because of the subject's self-movement (Gibson, 1950). Optic flow is characterized by movement of the entire visual field (whereas object movement only affects part of the visual field; e.g., Wurtz, 1998) in the opposite direction with respect to the observer's movement, providing information about the direction of self-motion and the arrangement and position of objects in space (e.g., Gibson, 1950). Optic flow is important even when combined with other movements, such as eye movements (e.g., Wurtz, 1998), in providing the observer with information about posture, orientation, and balance. Consequently, it plays a key role in regulating locomotor parameters that rely on accurate estimates of body displacement. Numerous studies have demonstrated that manipulating optic flow perturbs some gait speed and stability (Warren et al., 2001), influences step width and variability (Bruggeman et al., 2007), and induces adaptive locomotor responses mediated by visuomotor integration mechanisms (Lamontagne et al., 2007; Salinas et al., 2017). The relevance of optic flow becomes even more evident when considering age-related sensory decline. where older adults rely more heavily on visual cues, including optic flow, for postural and locomotor control, particularly when proprioceptive and vestibular inputs become less reliable with age (Woollacott & Shumway-Cook, 2002).

Cognitive processing during locomotion

The effect of locomotion on cognitive processes has been widely studied, mainly using cognitive-motor dual tasks (CMDT), in which cognitive and motor tasks are executed simultaneously. When a cognitive task is performed concurrently with walking, competition emerges between sensory, attentional, and motor systems, producing measurable interference effects consistent with the capacity-sharing and multiple-resource theories of dual-task (Petrizzo et al., 2022; Davranche & Audiffren, 2004; Dietrich & Sparling, 2004). Depending on the intensity, locomotion may affect performance in the concomitant cognitive task (e.g., Wang et al., 2013; Wohlwend et al., 2017). High-intensity running or cycling induces distortion (overestimation) of stimulus duration in a concurrent cognitive task (e.g., Petrizzo et al., 2022; Lambourne et al., 2012). The estimated distance of a target varies inversely with the speed of movement toward the target (Fini et al., 2017). The perception of peripersonal space is expanded when the subject is walking, and this distortion is influenced only by proprioceptive and kinematic parameters since the optic flow had no effect (Noel et al., 2015). High-intensity locomotion, such as endurance and exhaustion exercises, reduces performance in tasks on cognitive functions (Bue-Estes et al., 2008) and especially executive functions (Del Giorno et al., 2010; Dietrich & Sparling, 2004). Low-intensity exercise increases alertness levels (Arcelin et al., 1998; Davranche & Audiffren, 2004; Audiffren et al., 2008; Chmura et al., 1997; Paas & Adam, 1991; Collardeau et al., 2001), inhibitory capacity (Davranche et al., 2009; Ando et al., 2011; Olson et al., 2016; Finkenzeller et al., 2019), word learning (Amico & Schaefer, 2020), and cognitive flexibility (Oppezzo & Schwartz, 2014; Tomporowski & Audiffren, 2014; Murali & Händel, 2022). Positive effects of low-intensity physical activity on attention and memory processes were also found Rattray & Smee, 2016; Radel et al., 2018; Sanabria et al., 2011; Pesce et al., 2003, 2004).

Brain processing during CMDTs

None of the mentioned studies investigated the neural correlates of such changes in cognitive performance. However, other studies have examined the brain functions in the context of CMDT using the event-related potential (ERP) technique, measuring brain activity evoked by the stimuli of a cognitive task. Chen et al. (2022a,b) found that early processing associated with a visual discrimination task is enhanced during locomotion. Specifically, they found that the early N1 component amplitude was modulated by walking. Moreover, no difference in behavioral performance was detected between the walking and stationary conditions. In addition, Chen et al. (2022b) found a decrease in late cognitive processing (P3 component) while walking. The N1 increase was associated with a shift in attentional state related to visual awareness and a change in spatial visual processing during walking. Using an auditory discrimination task, Ladouce et al. (2019) found a lower P3 amplitude during treadmill or real walking than in a static position; while walking, accuracy rates were also lower than standing. A recent review (Schmidt-Kassow & Kaiser, 2023) considered 27 ERP studies and indicated that the N1 and the P3 effects are the most replicated outcomes, even though contrasting. However, most ERP studies have focused on methodological aspects, such as the ERP reliability during walking, running, or cycling, handling of noise and artifacts, or testing of mobile EEG systems without theory-driven aims.

One recent attempt in this direction was made by our group (Di Bello et al. 2024). We tested the effect of movement complexity on cognitive performance. Results revealed that taking a simple walking step before responding in a discriminative response task increased the N1 amplitude while reducing the P3. In contrast, simpler reaching movements did not. This effect was explained by considering that the resources needed to control movement and analyze the surrounding environment are taken away from those needed to perform the cognitive task. However, behavioral performance was not affected. Therefore, taking a simple step requires less cognitive effort than walking to achieve the same accuracy standards. Similar effects were found in the pre-stimulus phase by greater involvement of visual and motor preparatory processes (Casella et al., 2024). A subsequent study (Di Bello et al., 2025) showed that, compared to stationary position, treadmill walking improved accuracy and reduced the response time in the cognitive task, along with a concurrent increase in both cognitive and motor preparation in the pre-stimulus phase. The addition of optic flow further enhanced motor preparation and consequently reduced the response time. However, the presence of the flow field reduced cognitive preparation and accuracy. These results were interpreted within the framework of dual-task theories since optic flow, by requiring cognitive processing, draws cognitive resources away from the execution of the cognitive task, resulting in a performance decline.

Together, the evidence reviewed above highlights how locomotion, optic flow, and cognitive processing interact through shared and dynamically allocated neural resources. While several studies have examined cognitive–motor interference or visual motion processing separately, far fewer have investigated how optic flow modulates reactive cortical activity during walking, particularly within a dual-task context. Existing findings suggest that optic flow alters both early perceptual encoding and higher-order attentional processes, yet the precise mechanisms through which these modulations influence cognitive performance during locomotion remain poorly characterized. In particular, it is still unclear how reactive ERP components are jointly shaped by gait-related demands, visual motion processing, and the perceptual competition introduced by flow field stimulation. Addressing this gap is essential for refining theoretical models of perception–action coupling and cognitive–motor resource sharing.

In light of these considerations, the present study aims to: 1) confirm the effect of walking on post-stimulus reactive ERP components associated with early and late visual and attentional processes of a concomitant cognitive task; 2) verify whether optic flow can modulate such effects; 3) associate ERP component modulation to behavioral performance; 4) extend the Di Bello et al. (2025) result to reactive processing. To these aims, the present work will use the same experimental design as in Di Bello et al. (2025), comparing walking and standing with and without optic flow to test their possible interaction on brain processes. The addition of simulated optic flow (flow field) conditions served first to increase the realism of walking without losing the control and standardization ensured by laboratory testing. Second, it was aimed at distinguishing the effects of proprioceptive and somato-motor elements from those of purely sensory elements on cognitive processes and performance in a visual-discriminative motor task.

In contrast to previous ERP studies that have mainly focused on single components, the present work examined a broader range of ERP responses to provide a more comprehensive view of cognitive–sensorimotor interactions. Beyond the N1 and P3 components, we also included earlier components reflecting distinct stages of sensory and sensorimotor processing. Specifically, the parieto-occipital P1 and the prefrontal N1 (pN1), peaking around 120 ms. As previously done, we studied the parieto-occipital N1 but also the prefrontal P1 (Pp1), both peaking between 180 and 220 ms. The P1 and the N1 reflect early visual encoding processes within extrastriate visual areas and are sensitive to attention, motion, and optic flow (e.g., Brandt et al., 1998; Heinze et al., 1994; Luck, 2014; Pitzalis et al., 2012, 2013; Morrone et al., 2000). The pN1 and the pP1were associated with sensory awareness intended as subjective experience of the visual perception, and awareness of the sensory–motor integration, intended as conscious experience of the sensory–motor coupling, respectively, in the anterior insular cortex (e.g., Di Russo 2016; Gonçalves et al., 2018; Perri et al., 2018). The P3 is a complex activity associated with many post-perceptual processing, including attention and decision-making, and memory in temporal and parietal cortices (e.g., Polich, 2007). The study of these components together should allow for a finer-grained characterization of how walking and optic flow jointly influence concomitant processing of a cognitive task.

In line with previous studies (e.g., Cao et al., 2019), we expect to confirm that walking could enhance the N1 amplitude since it is associated with visual attention for the surrounding environment (Chen et al., 2022; Di Bello et al., 2024). If optic flow influences early visual and attentional processing, the presence of optic flow should also affect the P1 and the N1 (e.g., Heinze et al., 1994; Luck et al., 1990). Then, considering that walking may produce a shift in attentional state related to visual awareness (Chen et al. 2022a,b), we expect increased sensory (pN1) and sensorimotor (pP1) awareness during walking with optic flow, as more conscious resources are required for simultaneous activities. For the P3, we expect to replicate previous findings indicating small amplitudes during walking (Chen & Haendel, 2022; Ladouce et al., 2019; Di Bello et al., 2024). We have the same expectation for the presence of a flow field, since it could potentially divert resources away from stimulus evaluation (Palmisano et al., 2016; Kimura et al., 2015). Behaviorally, we expect greater accuracy during walking without optic flow because of the absence of visual-stimulus interference (Di Bello et al., 2025). Moreover, we expect a response time (RT) variability reduction, as walking stabilizes attention, reduces lapses (Legrand et al., 2020; Rahlf et al., 2019), and enhances sensorimotor coordination through proprioceptive, vestibular, and subcortical rhythmic signals (Angelaki & Cullen, 2008; Brandt et al., 1998; Zelaznik et al., 2002; Hegner et al., 2007), potentially aligning responses with walking pace and optic flow and increasing RT consistency.

9.2. Methods

9.2.1. Participants

The sample size was determined through a power analysis conducted using G*Power software (version 3.1.9.4). Parameters were set for a mixed-design analysis of variance (ANOVA), with a significance level (α) of 0.05, a statistical power of 0.95, and an effect size f(V) of 0.67. The effect size was derived from the average partial eta squared (η_p^2) reported in a previous study that employed a similar analysis (Lucia et al., 2023). Based on these settings, the required sample size was estimated at 40 participants. Accordingly, 40 volunteers were recruited from the student population of the University of Rome “Foro Italico”. The sample included 25 males and 15 females, with ages ranging from 20 to 36 years (mean age=24.5 years, SD=4.7).

Exclusion criteria were as follows: 1) presence of neurocognitive or motor disorders that could interfere with understanding instructions or performing the task; 2) severe visual impairments that could hinder stimulus discrimination (participants with minor, corrected vision issues were included).

All participants provided their informed consent before participating in the study and were unaware of the experimental objectives. The study was conducted in accordance with the World Medical Association’s Code of Ethics (Declaration of Helsinki, 1964) and was approved by the university’s ethics committee.

9.2.2. Visual Stimuli and Experimental Procedures

All participants performed a visuomotor discrimination task (DRT). Each stimulus was a 4°×4° grey square containing a pattern of 36 black segments (Figure 1). The two target stimuli consisted of horizontal lines and a grid of horizontal and vertical segments. The two non-target stimuli included vertical lines and a rotated version of the same grid, turned 90° to the left compared to the target stimuli. Each stimulus was displayed for 250 milliseconds, with a variable inter-stimulus interval ranging from 2200 to 3200 ms.

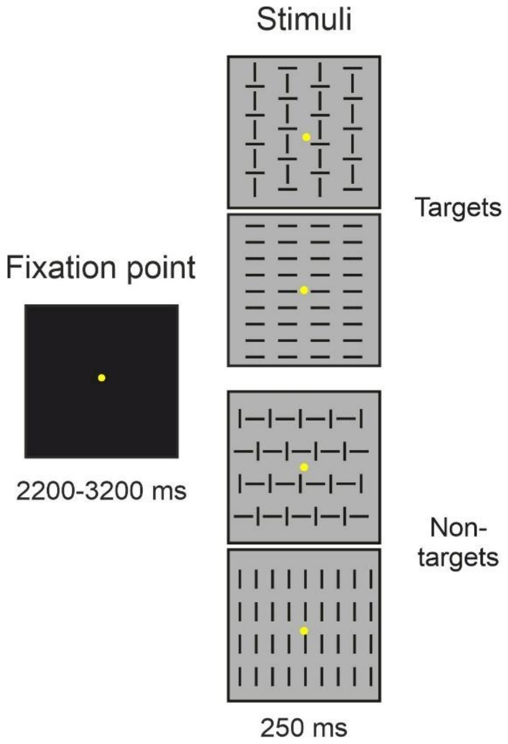

Figure 1. Schematic representation of the discrimination response task (DRT). In each trial, one of the four illustrated stimuli was presented.

During the DRT task, participants were instructed to pay close attention to a sequence of visual stimuli (two targets and two non-targets) which appeared one at a time in rapid succession. They were asked to press a button as quickly and accurately as possible whenever one of the two target stimuli appeared, and to withhold their response when a non-target was shown (Go/No-go task).

The DRT task was performed in front of a 32-inch screen placed 114 cm from the participant's eyes, covering a visual field of 35.4° horizontally and 31.7° vertically. A fixed central fixation point (0.15×0.15°) remained visible throughout the task.

All participants completed the DRT task during a single experimental session, under two distinct conditions (Figure 2): (1) walking on a treadmill (Walk condition), and (2) standing still on the treadmill (Still condition). The sequence of these conditions was counterbalanced across participants to control for learning and physical exertion effects. The response device was held in the right hand and operated with the right index finger. In the Walk condition, participants walked on a motorized treadmill (ISE®, model SY-1006) set to a constant speed of 1 km/h. The experiment was conducted in a dimly lit, sound-attenuated room.

Each run included 40 target and 40 non-target stimuli, presented in random order, resulting in a 50% target probability. Runs lasted approximately 3 minutes each, with a total of 10 runs per condition (still/walking). Short breaks were given between the two conditions, resulting in a total duration of around 90 minutes.

Furthermore, to assess the influence of realistic motion, participants were divided into two groups of 20 subjects each. As shown in Figure 2, one group (the Flow field group) performed the task while the stimuli were presented against a background video of dots moving radially outward, simulating optic flow consistent with walking at a speed of 1 km/h. The other group (No Flow field group) completed the task against a black background. A pseudo-randomized assignment was used to ensure a balance in age and sex between groups. Even though dot-based flow fields do not have higher-order scene information as real-world environments, converging evidence shows that dot-based flows engage the same brain network observed with richer scenes (e.g., Pitzalis et al., 2015).

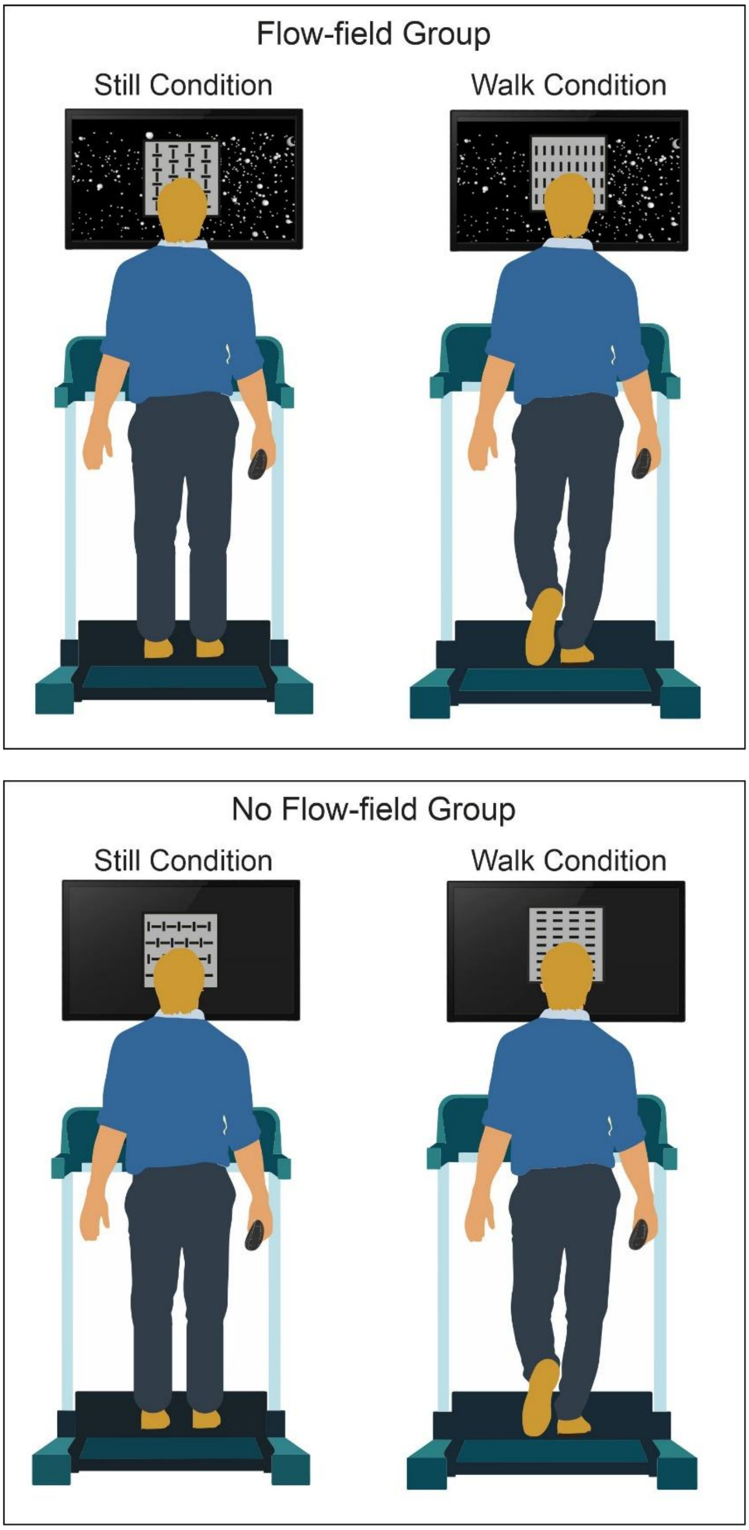

Figure 2: Schematic illustration of participants in the two experimental groups (Flow field group; No Flow field group) across the two experimental conditions (a. Walking; b. Still)

9.2.3. Behavioral Measures

Participant performance in the DRT was evaluated through three key behavioral indicators: the average response time (RT) to target stimuli, reflecting processing speed; the error rate (Err) used to evaluate accuracy, which encompassed both false alarms (incorrect responses to non-target stimuli) and omissions (when no response was given to target stimuli), and the RT variability, measured using the intra-individual coefficient of variation (ICV) calculated dividing the response time standard deviation by the response time.

9.2.4. EEG Acquisition and Processing

Before task execution, participants were fitted with a 64-channel EEG cap (ActiCap^{TM}) following the international 10-10 placement standard. EEG signals were recorded during task performance using three BrainAmp^{TM} amplifiers and Recorder 1.2 software, all from BrainProducts GmbH (Gilching, Germany). The reference for EEG recordings was set to the average mastoid electrodes. Oculomotor activity (EOG) was tracked through two bipolar electrode pairs: one placed horizontally at the outer edges of the eyes to monitor side-to-side movements and another vertically, above and below the left eye, to track blinks and up-down eye shifts. The electrodes' impedance was maintained below 5 KΩ. EEG and EOG signals were digitized at 250 Hz and initially band-pass filtered (0.01–80 Hz, second-order Butterworth filter) along with a 50 Hz notch filter to reduce electrical noise.

The following offline analyses were conducted using the Analyzer 2.3 software (BrainProducts GmbH, Gilching, Germany). The raw signal was further filtered using a second-order high-pass filter at 0.1 Hz and a low-pass filter at 60 Hz. Ocular artifacts were corrected automatically using the Gratton algorithm. Trials with signal exceeding ±70 µV (2.7%) were excluded from analysis. Channels that were either excessively noisy or showed flat signals were reconstructed via spherical spline interpolation from neighboring electrodes. In total, 25% of participants required no interpolation, while 20% had one channel interpolated, 18% had two channels interpolated, 15% had three, 14% had four, and 8% of participants required interpolation of five channels. The frequency of interpolated channels was similar across the experimental conditions. ERPs associated with the DRT stimuli were analyzed by segmenting the EEG in intervals from 200 ms before the stimulus onset to 1200 ms after. The interval from -200 to 0 ms was used as the baseline. Target and non-target trials were averaged separately.

To identify a-priori the spatial and temporal parameters of ERP analysis, the “collapsed localizer” approach (Luck & Gaspelin, 2017) was applied. A grand average across all participants and conditions was computed, and the global field power (GFP) was used to determine the time windows to be analyzed. As shown in Figure 3, the GFP identified three peaks at 120, 210, and 480 ms, and intervals around these peaks were determined by calculating 90% of the peak amplitude. In the earliest interval (112-132 ms), two foci of activity were present: the bilateral parieto-occipital positivity of the P1 component and the medial prefrontal negativity of the pN1 component. For each component, we included the electrode with the maximum amplitude (peak electrode) and those with at least 90% amplitude of the peak electrode. Accordingly, for the P1 and the pN1 components, PO9-PO7-PO8-PO10 and Fp1-Fpz-Fp2-AF3-AFz-AF4-F1-Fz-F2 electrodes, respectively, were used for the analysis. The same procedure was used for the following intervals. In the second interval (192-220 ms), the bilateral parieto-occipital negativity of the N1 component and the medial frontal positivity of the pP1 component were detected and were represented using the same electrode pools used for the P1 and pN1, respectively. In the third interval (444-512 ms), the wide medial central positivity of the P3 component was present and represented using C1-Cz-C2-CP1-CPz-CP2 electrodes.

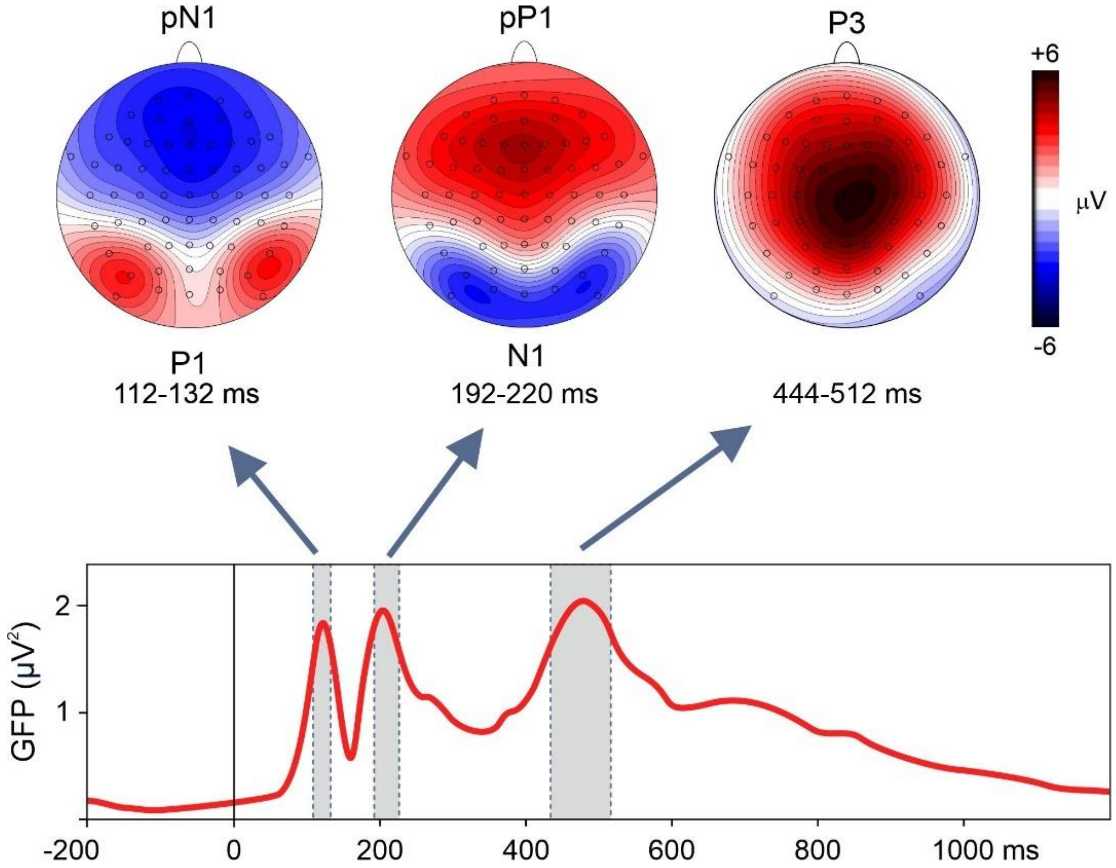

Figure 3: The graphic shows the GFP of the localizer with the selected interval highlighted. On top, the scalp voltage topography is shown for each interval.

9.2.5. Statistical analysis

Before conducting inferential analyses, the data were tested for normality and homogeneity of variance. Behavioral measures were examined using a 2×2 mixed-design ANOVA. Locomotion factor (Still vs Walk) was manipulated within-subjects, while Stimulation (Flow field vs No Flow field) was a between-subjects factor. When significant effects were found, Fisher's Least Significant Difference (LSD) and Bonferroni-corrected post-hoc comparisons were applied as appropriate. Statistical significance was set at $\alpha=0.05$, and the partial eta squared (η_p^2) was reported as a measure of effect size. ERP measures were examined using 2x2x2 ANOVAs with the Trial (Target vs. Non-target) as a further factor. All statistical analyses were performed using Statistica 11 (StatSoft Inc., Tulsa, OK, USA).

9.3. Results

9.3.1. Behavioural Data

The ANOVA carried out on response time showed non-significant differences between groups and conditions ($F_{(1,38)}<2.70$, $p>0.108$) with a mean value of 459 ms. See Figure 4a.

The ANOVA on response time variability (ICV) revealed a significant main effect of *Locomotion* ($F_{(1,38)}=5.66$, $p=0.02$, $\eta_p^2=0.130$) with less variability in the *Walk* (6.9% ±3.0) than in the *Still* condition (15.2% ±2.8). The effect of the *Stimulation* and the interaction between the two factors were not significant ($F_{(1,38)}<1.68$, $p>0.020$). See Figure 4b.

The ANOVA on response accuracy (error rate) showed a main effect of *Locomotion* ($F_{(1,38)}=7.45$, $p=0.01$, $\eta_p^2=0.164$), with fewer errors in the *Walk* (4.2% ± 5.4) than in the *Still* condition (6.7% ±8.2). The *Stimulation* factor was also significant ($F_{(1,38)}=4.08$, $p=0.05$, $\eta_p^2=0.097$), with a lower error rate in the *No-Flow field* (3.5%) than the *Flow field* (7.4%) condition. The interaction was not significant ($F_{(1,38)}=1.69$, $p=0.202$). See Figure 4c.

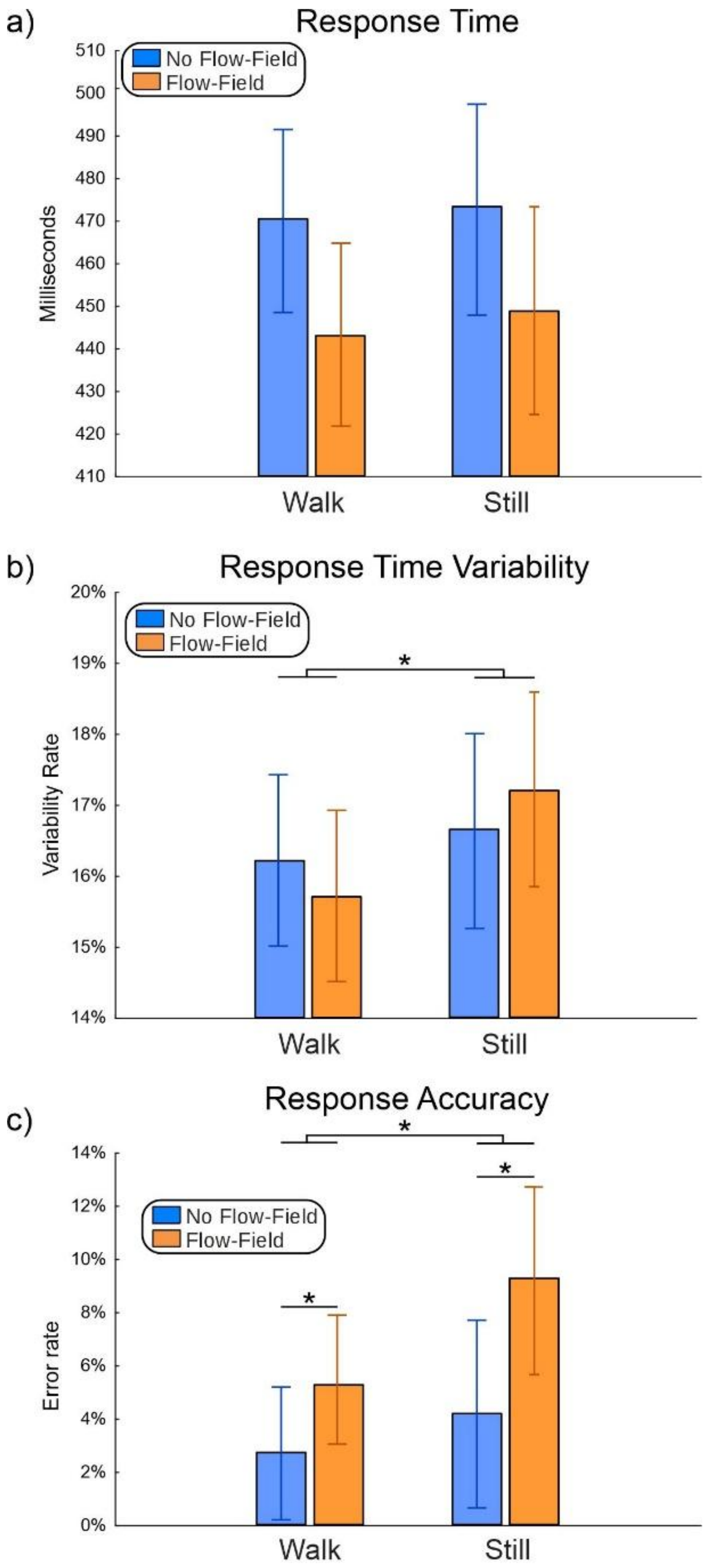

Figure 4: Comparison of behavioral data between the two groups (No Flow field vs. Flow field) across the two conditions (Walk; Still): a) Response time; b) Response time variability;

c). Response accuracy (error rate). Vertical lines denote the 0.95% confidence interval. *$p<0.05$.

9.3.2. ERP data

Figure 5 shows the ERP waveforms in the selected pool of electrodes representing the components studied for all conditions.

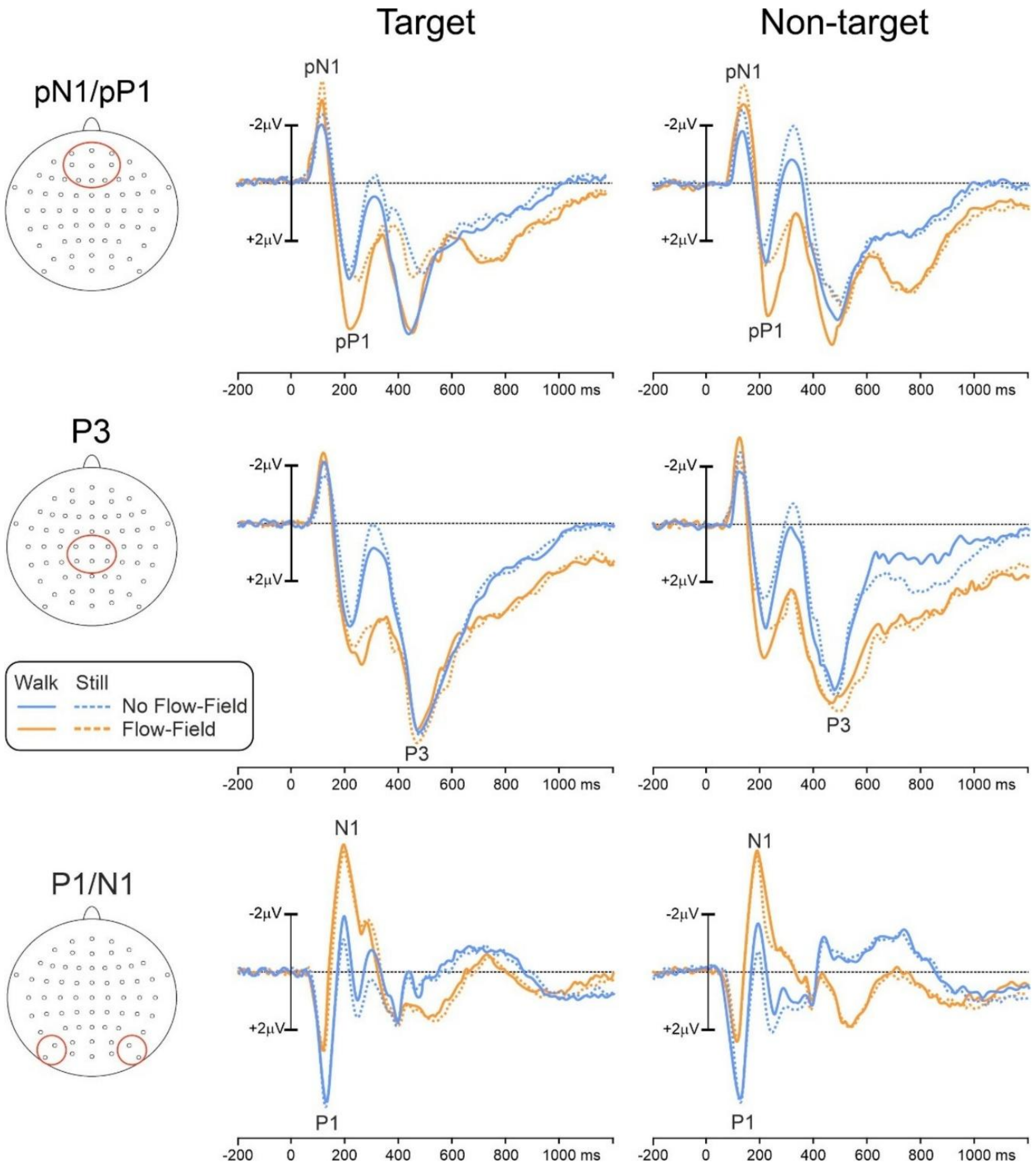

Figure 5: Grand-averaged ERP waveforms at (n=20) the selected electrode pools indicated in the head representations corresponding to the pN1 and pP1 (prefrontal pool: Fp1-Fpz-Fp2-AF3-AFz-AF4-F1-Fz-F2), the P3 (central pool: C1-Cz-C2-CP1-CPz-CP2), and the P1 and N1 (parieto-occipital pool: PO9-PO7-PO8-PO10) are shown for the two trial types (target and non-target) across conditions. The ERP components studied are labeled. Upward deflections indicate negative amplitudes.

As shown in Figure 6a, the ANOVA on the P1 component revealed a significant main effect of *Stimulation* ($F_{(1,38)}=13.93$, $p<0.01$, $\eta_p^2=0.268$), with greater amplitudes in the *No Flow field* compared to the *Flow field* conditions. The effects of *Locomotion* and *Trial* were not significant ($F<1$). The *Stimulation* × *Locomotion* ($F_{(1,38)}=20.15$, $p<0.01$, $\eta_p^2=0.347$), and the *Stimulation* × *Locomotion* × *Trial* ($F_{(1,38)}=4.29$, $p=0.05$, $\eta_p^2=0.102$) interactions, even though significant, did not add further information. The *Locomotion* × *Trial* interaction ($F_{(1,38)}<1$), was not significant.

As shown in Figure 6b, the ANOVA on the pN1 component showed a main effect of *Stimulation* ($F_{(1,38)}=16.43$, $p<0.01$, $\eta_p^2=0.302$) and *Locomotion* ($F_{(1,38)}=7.31$, $p=0.01$, $\eta_p^2=0.161$), indicating larger amplitudes in the *Flow field* than *No Flow field* condition and in the *Still* versus *Walk* condition. The *Stimulation* × *Locomotion* interaction was significant ($F_{(1,38)}=10.00$, $p<0.01$, $\eta_p^2=0.21$), however, post-hoc comparisons did not reveal any additional significant differences between conditions. The *Trial* effect and the other interactions were not significant ($F<1$).

As shown in Figure 6c, the ANOVA on the N1 component revealed a main effect of *Stimulation* ($F_{(1,38)}=11.73$, $p<0.01$, $\eta_p^2=0.24$), indicating a larger amplitude for the *Flow field* than the *No Flow field* condition. A significant main effect of *Locomotion* also emerged ($F_{(1,38)}=5.29$, $p=0.03$, $\eta_p^2=0.12$), indicating larger amplitude for the *Walk* than the *Still* condition. Furthermore, the *Stimulation* × *Locomotion* interaction reached significance ($F_{(1,38)}=3.88$, $p=0.06$, $\eta_p^2=0.09$) and post-hoc comparisons indicated that without the *Flow field*, the *Walk* condition had larger amplitudes than the Still condition ($p<0.05$), while in the presence of the Flow field, no differences between the *Still* and *Walk* condition were present.

As shown in Figure 6d, the ANOVA on pP1 revealed no main effects of *Stimulation* and *Locomotion* ($F_{(1,38)}<1.46$, $p>0.234$). A significant *Locomotion* × *Stimulation* interaction ($F_{(1,38)}=7.74$, $p<0.01$, $\eta p^2=0.17$) was found. Bonferroni post-hoc comparison revealed that the *Walk* condition with *Flow field* had the largest amplitudes ($p<0.05$) compared to the other conditions, which did not differ from each other. A main effect of Trial ($F_{(1,38)}=57.36$, $p<0.01$, $\eta p^2=0.60$) was also observed, with larger amplitudes for Target than Non-target trials. The other interactions were not significant ($F<1$).

As shown in Figure 6e, the ANOVA on the P3 component revealed no significant effects of *Locomotion* and *Stimulation* and their interaction ($F_{(1,38)}<1.84$, $p>0.183$). However, as shown in Figure 6f, the main effect of *Trial* was significant ($F_{(1,38)}=8.52$, $p<0.01$, $\eta_p^2=0.183$), with larger amplitudes for *Target* than for *Non-target* trials. A significant Locomotion × Trial interaction $F_{(1,38)}=6.66$, $p=0.01$, $\eta_p^2=0.149$), confirmed the main effect of *Trial*.

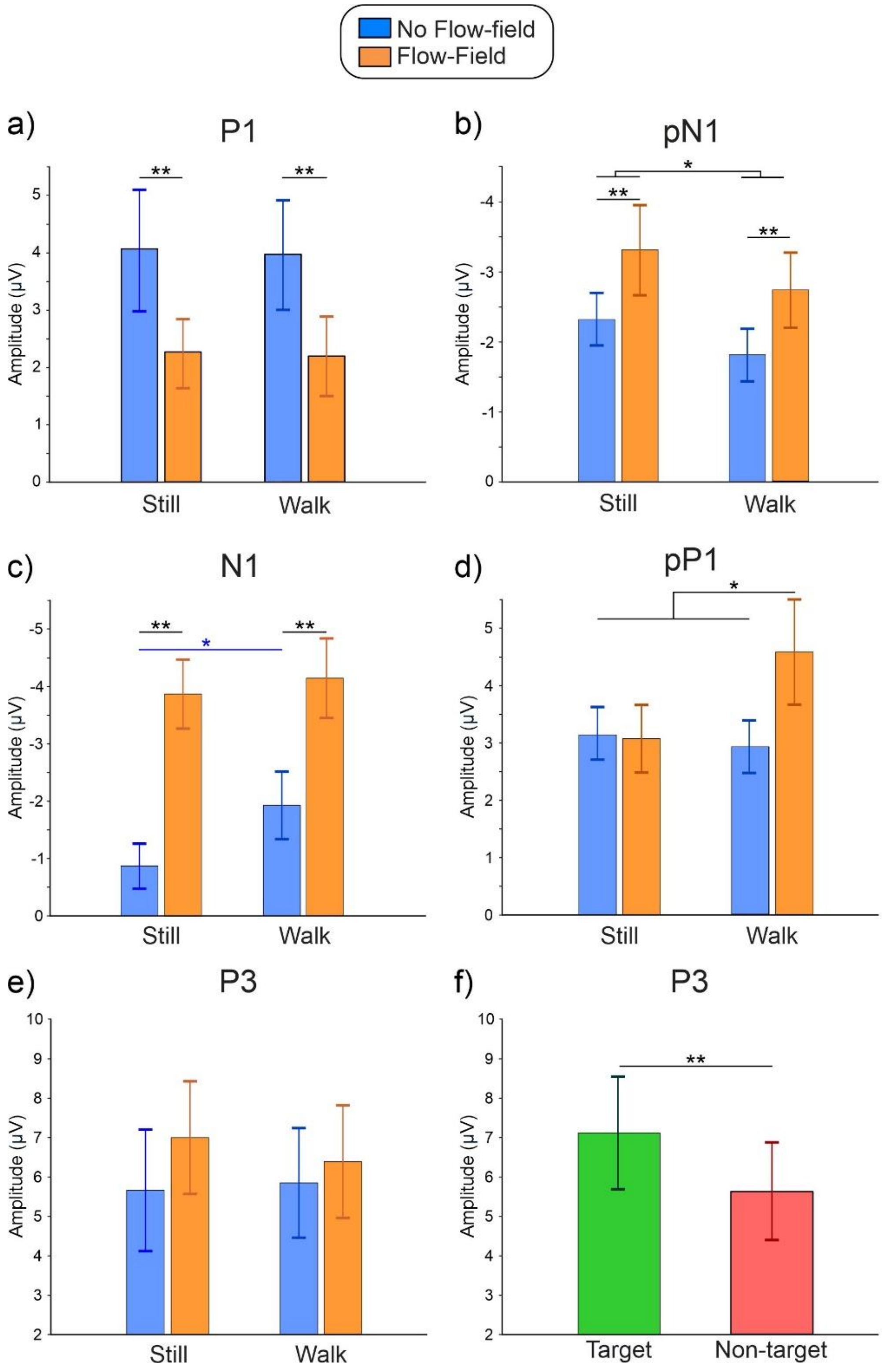

Figure 6. Mean amplitudes in all conditions for the a) P1, b) pN1, c) N1, d) pP1, and e-f) P3 components. The vertical bars indicate 0.95 confidence intervals. *$p<0.05$ **$p<0.01$.

9.4. Discussion

The present study investigated the effect of locomotion and optic flow on cognitive processing. This was achieved by analyzing both early and late ERP components, as well as behavioral performance, in a visuomotor cognitive task within the context of a cognitive-motor dual-task. This investigation was based on previous literature identifying a modulatory effect of walking on these processes. However, unlike previous studies, a further variable was tested in addition to walking on a treadmill: a flow field coherent with the direction and speed of walking. Optic flow induces vection, the illusory perception of self-motion, which can make walking appear more realistic.

From a behavioral standpoint, we confirmed literature (e.g., Schmidt-Kassow 2023; Di Bello et al., 2025) showing that low-intensity exercise, such as slow walking, may improve concomitant cognitive performance, increase response accuracy, and stabilize the response time. The presence of the simulated flow field stimulation did not affect the response speed but reduced the accuracy independently of the walking condition.

Regarding accuracy, results revealed a main effect of both locomotion and optic flow. Specifically, a reduction in error rate during walking and an increase in errors with the presence of optic flow were observed. Similar patterns were previously found by Di Bello et al. (2025), interpreted through the lens of Multiple Resource theory, which posits that the addition of a stimulus using the same sensory channel generates interference—a competition among various visual stimuli for access to conscious processing. The need to divide resources among multiple stimuli within the same sensory modality results in fewer available resources for each.

Regarding RTs, no significant effects were found, although —as previously shown by Di Bello et al. (2025)— we observed a trend: RTs were lower in the flow field condition. However, locomotion had a significant effect on ICV, a novel measure (not used in CMDT literature) that describes the response time variability. We analyzed the possible CMDT effect on ICV because the literature demonstrates that, from a cognitive perspective, walking helps maintain stable and consistent levels of attention, reducing mind wandering and lapses in vigilance, which underlie RT variability (Legrand et al., 2020; Rahlf et al., 2019). From a perceptual-motor perspective, during walking, coherent signals from the proprioceptive and vestibular systems contribute to improved sensorimotor coordination, increasing the consistency of motor responses (Angelaki & Cullen, 2008; Brandt et al., 1998). Moreover, walking, being a rhythmic activity, activates subcortical systems involved in motor control, as well as in temporal regulation and motor synchronization (Zelaznik et al., 2002; Hegner et al., 2007). Altogether, these mechanisms are expected to stabilize RTs and increase their consistency both within and between subjects, as response speed is likely to be synchronized with both walking speed and the optic flow itself.

The effect of walking

Walking was associated with the modulation of some ERP components evoked by the concomitant cognitive task, such as the pN1, the N1, and the pP1. While the pN1 was generally reduced during walking, the N1 and the pP1 were increased, but only in specific visual conditions, that is, without and with the presence of the flow field, respectively. The P1 and the P3 were unaffected by walking. The pN1 effect could be interpreted as a reduction of visual awareness for the cognitive task due to concomitant walking. However, this decline seems compensated, as previously found (e.g., Chen et al. 2022a,b), by an increase in attentional processing (indexed by the N1). In addition, we also found increased sensorimotor awareness over frontal areas (pP1).

The effect of the flow field

The flow field reduced the P1 amplitude and increased the pN1 and the N1 independently by walking. The pP1 was also increased by the flow field, but only during walking. Since P1 is associated with early visual processing, the presence of optic flow may have subtracted visual resources from the stimulus. A similar result was reported by Paluch and Wrobel (2016), finding P1 reduction when the evoking stimulus had dynamic backgrounds to induce vection. This effect was attributed to an increased perceptual load induced by the background. Consequently, fewer resources are focused on the foreground stimulus (see also Clark & Hillyard, 1996).

Since the pN1 has been associated with sensory awareness in frontal areas, and the N1 has been associated with attentional control in occipital areas, their increase is consistent with the hypothesis that optic flow acts as a distractor, generating interference and making early stimulus processing more difficult. As a result, greater cognitive effort and top-down control are needed (e.g., Luck, 2014; Vogel & Luck, 2000).

The P3 was unaffected by the flow field and only showed the typical Go/No-Go effect. Being larger for the target trials, which are more salient than the non-target trials requiring motor response (e.g., Mimnaugh et al., 2023; Roy et al., 2024). The lack of this effect could be explained by the slow and steady treadmill walking and flow field that did not pose additional post-perceptual processing demands on the performance of the cognitive task (For similar results, see Gramann et al., 2010).

Interaction between walking and the flow field

The pP1 was the largest while walking with the flow field. This was the condition that provides coherent input from multiple sensory systems: motor signals from walking, visual cues from the optic flow, proprioceptive feedback from joints and muscles, and vestibular input related to balance and spatial orientation. The coherence among these streams may have enhanced the engagement of frontal sensorimotor integration mechanisms, potentially reflected in the increased pP1 (e.g., Perri et al., 2018). This is consistent with previous findings indicating that sensorimotor congruency enhances early frontal activity (Babiloni et al., 2008). The pP1 modulation by walking might be attributed to the activation of motor-related brain areas during locomotion, facilitating the execution of other movements, such as the one required for response. Thus, less cognitive effort is needed, since these brain areas are already activated, requiring no additional energy to initiate them. In this case, the two tasks (walking and button-pressing) share the same (motor) resources, but rather than interfering with each other, one facilitates the other — consistent with the Shared Resource theory (e.g., Jeannerod, 2001) and Crosstalk Theory (e.g., Navon & Miller, 1987).

We found an opposite trend in the N1, a component associated with conscious visual processes. N1 was higher during walking compared to stillness in the absence of optic flow. With optic flow, however, this difference was not observed, since optic flow, as a stimulation of movement, makes walking more ecologically valid and replaces visual stimulation from the actual environment in the context of real locomotion (Thommai et al., 2021; Prokop et al., 1997). Alternatively, the amplifying effect of walking on the N1 disappeared in the presence of the flow field, possibly because the simulated optic flow, made of moving dots, may have distracted the participant from the cognitive task. This is because, in a noisy context such as the one generated by optic flow, greater attentional and visual effort is needed to discriminate signal from noise and detect targets amid distraction. Increased sensory competition between the target and moving background requires more attentional focus to isolate the relevant target. Future studies using naturalist optic flow instead of dots could confirm this interpretation.

The study has some limitations: Locomotion in the present protocol was performed at 1 km/h, a speed chosen to preserve EEG signal quality during walking, but slower than natural walking;

prior work shows that locomotor speed modulates sensory–motor coupling and the neural correlates of gait control (Li et al., 2022), thus potentially limiting ecological generalizability. The use of a between-subjects manipulation of optic flow, while motivated by the need to avoid adaptation, vection, and carryover effects that commonly occur with repeated exposure to wide-field motion (Kim & Palmisano, 2010), introduces unavoidable susceptibility to individual-difference variability. Although random assignment and baseline equivalence checks mitigate this risk, between-group heterogeneity cannot be eliminated, and future studies would benefit from complementary within-subjects or crossover designs combined with strategies to limit visual-motion aftereffects (Tucker-Drob, 2011). Together, these considerations outline the boundary conditions within which the present findings should be interpreted and highlight important directions for future, more ecologically grounded investigations.

In conclusion, this study confirmed previous findings from our group (Di Bello et al., 2025) and other studies regarding the improvement of cognitive performance induced by walking. Here, we found that walking on a treadmill while executing a cognitive task affects brain processing, improving task performance. This improvement due to walking seems to stem from increased early cortical activity facilitating cognitive task execution. In a CMDT context, this means that slow walking may improve cognitive performance since the simultaneous activation of more brain areas than a single task may result in the formation of new circuits specifically supporting their combined execution, ultimately facilitating performance in both tasks when performed together (Erickson et al., 2007; Bherer et al., 2005). On the other hand, we found a worsening of cognitive performance induced by the introduction of moving dots in the background simulating a forward optic flow. We suggest that this result is likely due to increased cognitive load. This hypothesis is corroborated by the reduced visual processing in the occipital cortex compensated by increased frontal activity, an indication of greater cognitive resource investment in the presence of optic flow. We confirmed that walking may increase attentional processing on a concurrent cognitive task, but we also found that walking may also increase sensorimotor awareness. This suggests the idea that coherent signals from different sensory channels should contribute to increased sensorimotor awareness, allowing for accurate and consistent behavior.

10 General Discussion

The studies presented in this dissertation offer a comprehensive exploration of how the brain integrates cognitive demands with motor control, particularly in dynamic and ecologically valid situations. A recurring theme throughout the work is the delicate balancing act the brain performs when it is simultaneously engaged in a cognitive task and in planning or executing movement.

What emerges from these experiments is a picture of the brain as a dynamic system that continuously reallocates its resources according to context. When participants were asked to perform a visual discrimination task while simultaneously walking or preparing a complex motor response, the brain did not simply split its attention evenly. Instead, it flexibly adapted—boosting early sensory and motor-related processes while scaling down later cognitive evaluation. This redistribution was especially marked in the presence of optic flow, which appeared to function both as a facilitator of ecological motor preparation and as a sensory competitor that taxed attentional resources.

From a neural perspective, this interplay was reflected in distinct shifts in activation patterns. The presence of optic flow consistently engaged a network of multisensory brain regions, including the cingulate sulcus visual area (CSv), parieto-insular cortex (PIC), and human PEc (hPEc). Each of these areas contributed in a specific way to the integration of visual motion with bodily signals. CSv responded robustly to coherent optic flow patterns and appeared to serve as a stable anchor for interpreting self-motion, largely unaffected by mismatches between visual and proprioceptive cues. PIC, in contrast, was more sensitive to conflict—especially when the visual motion conveyed by the optic flow did not align with actual bodily movement. This region's known role in visuo-vestibular integration likely supports its function in resolving such sensory discrepancies. hPEc also showed heightened sensitivity to incongruent sensorimotor input, reflecting its role in recalibrating internal models of body position and trajectory.

In conditions of dual-task interference, these multisensory hubs become particularly important. Their engagement suggests that the brain is not simply responding to the sum of visual and motor inputs, but is actively comparing them—generating predictions, detecting mismatches, and adjusting behavior in real time. Such mechanisms are consistent with predictive coding theories, which propose that perception and action are tightly coupled through continuous loops of expectation and correction.

Beyond the realm of sensory integration, the studies also revealed how the brain prioritizes its limited attentional and cognitive resources under complex conditions. As participants moved from simpler tasks (like a keypress) to more complex actions (such as stepping), early perceptual components—such as the P1 and N1, typically generated in occipito-parietal regions like V3A, MT/V5, and the posterior intraparietal sulcus—increased in amplitude. This suggests a preparatory upregulation of the perceptual system, as if the brain were heightening its sensory readiness to support the upcoming action.

However, this initial sensory enhancement came at a cost. Later components, particularly the P3, which reflects stimulus evaluation and decision-making and is often associated with activity in the dorsolateral prefrontal cortex (DLPFC) and posterior parietal cortex (PPC), were significantly attenuated. This pattern of results points to a classic cognitive-motor trade-off: when the motor system requires more attention and resources—as during walking or complex full-body movements—the cognitive system yields, reducing its investment in high-level evaluative processes.

Perhaps most telling was the emergence of a late negative ERP component—known as N750—which became more pronounced as motor complexity increased. This component is thought to reflect late-stage motor planning and is often linked to medial frontal structures like the supplementary motor area (SMA) and cingulate motor areas (CMA). Its modulation across conditions supports the idea that motor demands are not passively managed but are actively prioritized and prepared for, especially when the surrounding visual environment, via optic flow, signals the need for balance and coordination.

Interestingly, while these neural shifts were clearly observable, they did not always correspond to reductions in behavioral performance. In many cases, participants maintained their accuracy even under complex conditions, suggesting that the brain's resource reallocation is effective and strategic rather than detrimental. The increased recruitment of anticipatory motor regions (e.g., pre-SMA) and early visual-perceptual areas appears to compensate for the downregulation of executive systems, ensuring that performance is preserved even when demands are high.

This capacity to maintain performance under dual-task load underscores the flexibility of the neural system. Rather than treating motor and cognitive processes as separate and competing, the brain seems to manage them through context-dependent integration. The motor system is not just a recipient of cognitive commands, nor is cognition isolated from bodily states. Instead, these systems co-regulate each other, with multisensory integration hubs like CSv, hPEc, and PIC acting as key sites of convergence where decisions about resource allocation are made.

This understanding has clear implications. From a theoretical standpoint, it expands the scope of dual-task models, grounding them not just in attentional competition but in sensorimotor integration and ecological adaptation. From a practical perspective, these findings can inform rehabilitation strategies, especially for populations with impaired balance, executive function, or sensory integration. Similarly, in applied domains such as sports or virtual reality, knowing how optic flow and movement complexity shape cognitive-motor dynamics can guide the design of training or interfaces that align with the brain’s natural priorities.

In sum, the brain’s response to dual-task demands is not merely reactive—it is proactive, predictive, and deeply tied to the structure of the body and the nature of the surrounding environment. Optic flow, as used in these experiments, does more than simulate motion: it activates the very circuits that support the tight integration of seeing, moving, and thinking. And by studying how these circuits respond under pressure, we gain a clearer view of the brain’s remarkable ability to balance the needs of perception, action, and cognition in real time.

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