











Universidade do Minho

Université de Lille Ecole Doctorale Sciences de l'Homme et de la Société Faculté PsySEF – Psychologie et sciences de l'Education et de la Formation SCALab-UMR CNRS 9193

Universidade do Minho Centro de Investicação em Psicologia School of Psychology Psychological Neuroscience Laboratory

# THE INTERPLAY BETWEEN OBJECT OWNERSHIP AND PERIPERSONAL SPACE: BEHAVIORAL, NEUROPHYSIOLOGICAL AND NEUROIMAGING EVIDENCE

Interaction entre le sens de la propriété des objets et l'espace péripersonnel : études comportementales, neurophysiologiques et en neuroimagerie

Thesis submitted and defended by Lucie Lenglart

For the degree of Doctor in Psychology

Supervised by Pr. Yann Coello, Pr. Adriana Sampaio, and Dr. Clémence roger

The 3rd of October 2025

#### Jury members:

Pr. Michael ANDRES	Université Catholique de Louvain	Rapporteur
Pr. Matthew LONGO	Birbeck University of London	Rapporteur
Pr. Ana P. PINHEIRO	Universidade de Lisboa	Examiner
Pr. Yann COELLO	Université de Lille	Supervisor
Pr. Adriana SAMPAIO	Universidade do Minho	Co-supervisor
Dr. Clémence ROGER	Université de Lille	Co-supervisor

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Engineer: Is this a holdup?

Doc: It's a science experiment!

— Back to the Future III

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#### **ABSTRACT**

We interact daily with objects in our surroundings that are physically close and that can be acted upon. These objects are located within our peripersonal space (PPS), a space that serves as a motor interface between the body and the environment for interaction. Objects within the PPS are automatically encoded in sensorimotor terms, as if the organism were anticipating an interaction with them. However, objects in our PPS do not always belong to us, and we cannot interact with them. This situation may lead to a conflict between (1) the sensorimotor coding of objects that contributes to action preparation toward reachable objects in the PPS, and (2) the conceptual ownership-based coding of objects, which indicates that interacting with some objects is favored, and interacting with others is forbidden. In this context, the interaction between PPS and ownership in object processing remains poorly understood.

To examine this hypothesis, a series of behavioral and neuroimaging studies was conducted using reachability judgment tasks. In these tasks, participants evaluated whether objects, labelled as self- or other-owned, were within reach when placed at different distances. The first study provided behavioral evidence of an interaction between ownership and space, with faster response times observed for self-owned objects. This facilitation effect was restricted to PPS and was accompanied by an expansion of the perceived boundary of reachable space. The second study further defined this interaction by showing that better inhibition control, serving efficient action, was facilitated for self-owned objects in PPS. Finally, studies 3 and 4 highlighted the temporal and neural correlates of the observed effects. EEG data indicated that PPS influenced early perceptual processing, while ownership affected later, post-perceptual stages, suggesting a sequential process from spatial encoding to the integration of higher-order conceptual information. fMRI results showed that objects in PPS activated parietal regions involved in sensorimotor processing, with stronger responses for self-owned than other-owned objects. Additionally, they showed that activations in the ventral and dorsal mPFC differentially coded for self-owned objects in a context-dependent manner.

Together, these findings demonstrate that the processing of objects in PPS is not governed solely by its physical proximity or low-level salience, but is also modulated by higher-order factors such as ownership. In this framework, in PPS, ownership constitutes a contextual cue that modulates action selection by pointing not only to what is physically accessible, but also to what is socially relevant.

*Keywords:* Peripersonal space, Object ownership, Perception-action coupling, Self-relevance, Social context, EEG, EMG, fMRI

## **PUBLICATIONS**

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## **Abbreviations**

ACC Anterior cingulate cortex

AIP Anterior intraparietal area

PFC Prefrontal Cortex

dlPFCDorsolateral prefrontal cortexvmPFCVentromedial prefrontal cortexdmPFCDorsomedial prefrontal cortex

POS Parieto-occipital sulcus

vPOS Ventral parieto-occipital sulcus dPOS Dorsal parieto-occipital sulcus

EEG Electroencephalography

EMG Electromyography

EPS Extrapersonal space

ERP Event-related potential

fMRI Functional magnetic resonance imaging

IFG Inferior frontal gyrus

IPL Inferior parietal lobule

IPS Intraparietal sulcus

aIPS Anterior intraparietal sulcus

LIP Lateral intraparietal area

MVPA Multivariate pattern analysis

PM Premotor

PMv Premotor ventral PMd Premotor dorsal

PPC Posterior parietal cortex

PPS Peripersonal space

pSTS Posterior superior temporal sulcus

SAN Self-attention network

SMA Supplementary motor area

SPL Superior temporal sulcus

TMS Transcranial magnetic stimulation

VIP Ventral intraparietal area

## General

e.g. Exempli gratia

Etc. Et caetera

i.e. Id est

v.s. versus



## Part I THEORETICAL FRAMEWORK

#### 1.1. A functional segmentation of space

#### The space surrounding the body

#### 1.1. A FUNCTIONAL SEGMENTATION OF SPACE

It is crucial, for every human being, to be able to extract the critical elements from the abundance of information available in their environment. To navigate this complexity, they must continuously extract information from their surroundings, filtering the vast array of sensory inputs to identify what is most important for their current state or future actions. For example, a piece of food may demand attention, a looming obstacle may require avoidance, or a familiar face may invite social interaction. This ability to focus on meaningful features of the environment is fundamental to how organisms engage with the world. By transforming a chaotic flow of stimuli into actionable insights, organisms actively shape their perception of the environment. In this way, in order to anticipate and perform an appropriate motor action, our brain does not process space as a unitary continuum, but as multiple and nested spatial maps (Previc, 1990, 1998) which are implicitly divided following functional characteristics.

#### 1.1.1. Early models of spatial organization

Over time, evidence accumulated in favour of a functional division of space, grounded in the observation that humans and non-human animals interact differently with objects depending on their distance. Brain (1941) pioneered this idea by introducing the concept of a "grasping distance" distinct from a "walking distance". This theoretical proposition emerged from clinical observations of patients with neurological impairments that affected spatial cognition and motor behaviour. Brain documented the case of patients who could interact with objects within arm's reach, but struggled to navigate or interact with objects in more distant spaces. Conversely, another patient showed the reverse pattern: he did not struggle in navigating space, but presented troubles when localizing objects within his reach. This double-dissociation suggested that different brain systems

#### 1.1.1. Early models of spatial organization

mediate these mechanisms, with the grasping distance corresponding to regions responsible for visuomotor coordination and object manipulation, while walking distance engaged systems related to spatial navigation and locomotion.

Following Brain's initial framework, several models have refined the distinction between these grasping and walking spaces. Notably, Grüsser (1983) first theorized an action-oriented model of spatial representation, where space is divided into a personal space (i.e., the space occupied by the body) and an extrapersonal space (i.e., the space extending beyond the physical boundaries of the body). This extrapersonal space<sup>1</sup> was further subdivided into different subspaces based on the potential for action. Organized along a proximal-to-distal gradient, these subspaces include (I) the grasping space (were interaction with objects is directly possible), (II) the instrumental grasping space (an extension of the grasping space available through tool-use) (III) the near-distant action space (where we represent precisely elements in space, up to approximately 8 m), (IV) the far-distant action space (beyond 8 m), and (V) the visual background encompassing elements such as the sky. This action-centred model emphasizes that action possibilities systematically decrease with increasing radius from the body, and that spatial perception is intrinsically linked to the capacity for action. In the same vein, Cutting and Vishton (1995) proposed a theoretical model focused on the ecological and perceptual differentiation of space. They suggested three distinct regions: the personal space surrounding the body, the action space within reachable distance, and the vista space extending beyond reach, typically encompassing

<sup>&</sup>lt;sup>1</sup> Here, the term "extrapersonal space" is used as defined by Grüsser, i.e., the space outside the direct physical boundaries of the body. However, a part of this space (notably the grasping space) can be included into what will be called hereafter the peripersonal space, which is distinct from the current prevailing definition of extrapersonal space.

#### 1.1. A functional segmentation of space

navigational environments. Their model emphasized significant differences in the perceptual cues and actions associated with each spatial domain: the action space is primarily supported by fine-grained and binocular visual input, whereas the visa space relies more heavily on monocular and dynamic visual cues. Nonetheless, the neurofunctional foundations of these spaces remained elusive, and their spatial boundaries were determined somewhat arbitrarily. For instance, the action space was proposed to extend up to 30 meters, corresponding to the space where individuals can act directly or throw objects, while the personal space is limited to 2 meters, allowing for more static forms of interaction.

To address these shortcomings, Previc (1998) expanded on these ideas with a model integrating functional and neurobiological considerations. From a neuropsychological perspective, he sought to explain the imbalance observed in the cardinal division of spatial processing in various neuropsychological disorders. To do so, he proposed four spatial zones: peripersonal, focal extrapersonal, action extrapersonal, and ambient extrapersonal spaces, each associated with distinct neural substrates, neurochemical activations, and behavioral purposes (Figure 1). According to Previc, the peripersonal space is specialized for immediate object manipulation and is represented in the premotor and parietal cortices. In contrast, the focal extrapersonal space, used for visual search and the recognition of objects and faces, engages attentional and visuospatial processing in regions such as the dorsal parietal cortex. Lastly, the action extrapersonal space supports navigation and orientation, relying on parietal and subcortical areas, while the ambient extrapersonal space facilitates situational awareness and postural control, associated with vestibular and brainstem structures.

#### 1.1.2. Contemporary perspectives: toward a dynamic gradient model of space

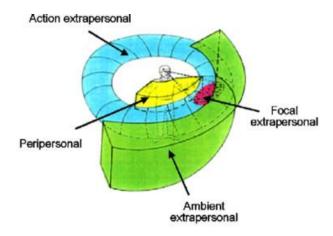


Figure 1. Graphical representation of Previc's theoretical model of the four behavioral spaces: peripersonal space (in yellow), focal extrapersonal space (in red) action extrapersonal space (in blue), and ambient extrapersonal space (in green). Reproduced from Previc (1998; 2006).

#### 1.1.2. Contemporary perspectives: toward a dynamic gradient model of space

The number and nature of functionally distinct spatial representations remain open questions, with several competing models proposed over the years (e.g., Hyvärinen & Poranen, 1974; Leinonen & Nyman, 1979; de Vignemont & Farnè, 2024; Bufacchi & Iannetti, 2018). Among the various models proposed, there is an agreement on a core distinction between extrapersonal space (hereafter EPS) - referring to regions beyond the immediate reach of the body, primarily involved in visual exploration, spatial orientation, and navigation - and peripersonal space (PPS), which encompasses the space within arm's reach, where direct interaction with objects is possible. As noted by Bufacchi and Iannetti (2018), these spaces are not defined by rigid boundaries; rather, they reflect dynamic, functional representations of space shaped by context and task demands. In this view, spatial representations such as PPS and EPS do not map directly onto fixed physical distances. Indeed, the same physical location may be processed as either peripersonal or extrapersonal depending on behavioral relevance and sensorimotor contingencies (Cléry et al.,

#### 1.2. Neural foundations of peripersonal space

2015). Importantly, current models suggest that PPS is not an all-or-nothing construct but follows a continuous, gradient-like structure (see Graziano & Cooke, 2006, for a review). This representation is formed through the multisensory integration of information from visual, auditory, tactile, vestibular, proprioceptive, and somatosensory modalities (Makin et al., 2007; Previc, 1998; Van der Stoep et al., 2016). This integration of multiple sensory signals supports a representation of space shaped by the opportunities for immediate interactions afforded by the environment to the body. For instance, motor control theories suggest that the motor actions prompted by these affordances entail the internal prediction of their tactile consequences (Shadmehr et al., 2010; Wolpert et al., 2011). As such, it has been proposed that PPS consists of multiple and possibly overlapping functionally-specialized subspaces. Each of these subspaces, whose associated mechanisms are anchored in action, carries distinct behavioral significance depending on whether the action goal is defensive or purposeful (Bufacchi & Iannetti, 2018). To avoid any confusion among these multiple constructs, I will throughout this thesis not use the term peripersonal space to refer to a strict Euclidean distance or to a fixed spatial measurement. Instead, I will use it to describe the space encoded by the brain as immediately surrounding the body, based on specific multisensory and motor-related mechanisms. I will refer to this encoding as peripersonal representation.

#### 1.2. NEURAL FOUNDATIONS OF PERIPERSONAL SPACE

#### 1.2.1. Neurophysiological origins of a somato-motor representation of space

The concept of PPS was first coined by Rizzolatti and colleagues (1981a, 1981b, 1981c) through single-cell electrophysiological recordings in macaque monkeys. In these foundational studies, they identified neurons in the prefrontal periarcuate cortical regions that responded to both tactile stimulation of specific body parts and to visual stimuli presented in the vicinity of these

#### 1.2.1. Neurophysiological origins of a somato-motor representation of space

same body regions (Figure 2). These multisensory neurons could be grouped into two functional categories based on the spatial extent of their visual receptive fields. The first group, termed pericutaneous neurons (54% of the multisensory neurons), responds to stimuli within 10 cm of the body surface (Rizzolatti et al., 1981b). The second, termed the distant peripersonal neurons (46% of the multisensory neurons; Rizzolatti et al., 1981b), respond to stimuli located slightly farther away, yet still within reachable space. In the ventral premotor area (area F4, located in the inferior part of area 6), approximately 85% of tactile neurons in F4 exhibit this bimodal responsiveness (Gentilucci et al., 1988), which allows for the integration of tactile and visual information within a common spatial framework. These neurons were mainly organized in a somatotopic manner, coding for distinct body parts such as the face, neck, arms, and hands.

Further research identified additional populations of multisensory neurons in parietal regions. For instance, neurons in area 7b of the inferior parietal cortex (Hyvärinen & Shelepin, 1979; Robinson & Burton, 1980) and the ventral intraparietal area (VIP) (Avillac et al., 2005; Colby & Duhamel, 1996; Colby et al., 1993; Duhamel et al., 1998) also exhibit integration of visual, tactile, and auditory signals. These parietal areas are thought to serve as key hubs for multisensory integration, and to support the construction of spatial representations crucial for bodily awareness, body-space interplay, and sensorimotor coordination (Avillac et al., 2004, 2005, 2007; Bremmer et al., 2001; Guipponi et al., 2013).

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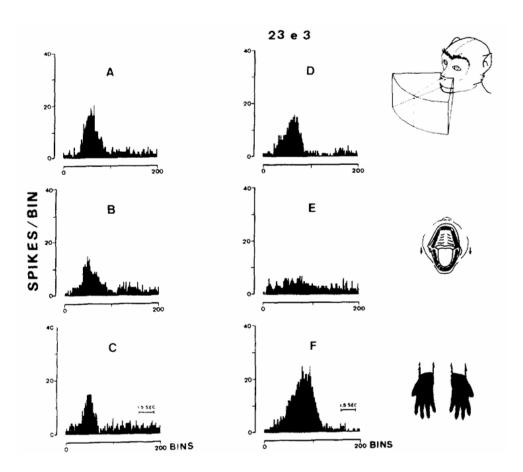


Figure 2. Responses of a distant peripersonal neuron in the posterior periarcuate cortex to visual, tactile, and proprioceptive stimuli (responsive regions shown on the right). (A) Tactile response to stimulation of the lower teeth with a cotton tuft. (B, C) Responses to ipsilateral and contralateral hand stimulation with a 2cm ball. (D) Visual response to the same ball moved toward the ipsilateral hand without contact. (E) Visual response to a large stimulus (black disk) approaching without contact. (F) Response to the ball introduced into the mouth. Histograms represent the sum of 10 trials. Reproduced from Rizzolatti (1981c).

Importantly, these multisensory neurons can adopt a range of anchoring schemes. In both premotor (F4) and parietal (VIP, 7b) regions, many visuotactile neurons are anchored in a body-part-centred reference frame: their visual receptive fields move congruently with the stimulated body region, such as the hand, face, or head, maintaining spatial alignment between the tactile and visual components of a given stimulus (Duhamel et al., 1998; Fogassi et al., 1996; Graziano et al., 1997). This organization ensures that visual events near a specific effector are continuously tracked despite postural changes, and supports precise sensorimotor coupling during both action and

defence. In area VIP, for example, the receptive fields of multisensory neurons are often aligned with head-centred or gaze-centred coordinates (Avillac et al., 2005; Bremmer et al., 2001). Additionally, while some visual responses in parietal and premotor PPS neurons exhibit retinotopic characteristics, their tight coupling with tactile or proprioceptive inputs suggests a transformation into body-related coordinates for functional integration (Avillac et al., 2005; Graziano & Gross, 1993).

Finally, beyond cortical areas, PPS coding extends to subcortical structures like the superior colliculus and the putamen. In the superior colliculus, neurons integrate visual and tactile stimuli, contributing to multisensory spatial representations critical for orienting body responses (Stein & Meredith, 1993). In the putamen, neurons respond not only to passive sensory stimulation but also during motor activity, suggesting a role in action preparation and execution (Graziano & Gross, 1993).

PPS multisensory neurons are thus distributed across multiple brain regions, which support distinct albeit related functional roles. Psychophysiological evidence delineates a complex, multifaceted construct driven by the integration of multisensory stimuli surrounding the body. This ability enables these neurons to integrate inputs from different sensory modalities, provided they occur simultaneously and with spatial congruency (Avillac et al., 2005). Though few studies demonstrated a true phenomenon of multisensory integration in PPS neurons (i.e., responses exceeding the sum of unisensory inputs; Avillac et al., 2007; Stein & Stanford, 2008), patterns of cross-modal facilitation and non-linear responses nonetheless support their role in multisensory processing (Bernasconi et al., 2018; Cléry et al., 2017; Noel et al., 2015, 2018). This integration is crucial for representing the boundaries of the body, contributing to body ownership (Ehrsson, 2012), to the localization of the self in space (Holmes & Spence, 2004; Noel et al., 2015), and

#### 1.2. Neural foundations of peripersonal space

shaping the body schema for action (Cardinali et al., 2009; Maravita et al., 2003). Notably, some PPS neurons respond to stimuli at a distance, extending the spatial scope of the body schema and supporting anticipatory activation, likely for predicting incoming touch (Gentilucci et al., 1988; Hyvärinen & Poranen, 1974).

#### 1.2.2. Neural correlates of peripersonal space in monkeys

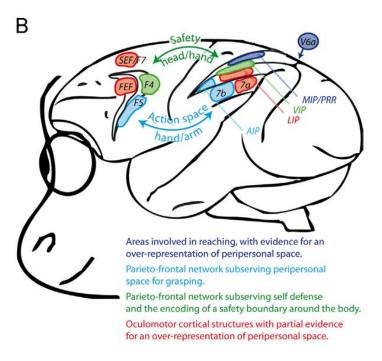


Figure 3. Functional networks associated with an enhanced representation in PPS. Areas in dark blue are involved in reaching, areas in cyan are part of a parieto-frontal network supporting representation of PPS for action, areas in green are part of a fronto-parietal network supporting representation of PPS for self-defence and the encoding of a safety boundary, and areas in red are oculomotor structures over-represented in the processing of visual information in PPS. Reproduced from Cléry et al. (2015)

#### 1.2.2. Neural correlates of peripersonal space in monkeys

In parallel with electrophysiological studies, lesion studies in monkeys provided evidence for separate neural substrates supporting PPS and EPS. Rizzolatti et al. (1983) showed that ablation of the postarcuate premotor cortex impairs the detection and grasping of nearby objects in the contralateral hemifield, affecting both somatosensory and visual processing. In contrast, lesions to the frontal eye fields primarily disrupted attention and exploratory eye movements in far space. These findings support the existence of separate spatial maps governing specialized behaviours in near and far space, and paved the way for researchers to begin exploring how distinct brain areas coordinate the processing of stimuli in PPS (Coello, 2024).

Building on physiological, lesional, and behavioral studies, researchers proposed models of PPS emerging from a specialized parieto-frontal network that transforms multisensory signals into motor-relevant representations. Synthesizing two decades of empirical work and theoretical propositions, Cléry et al. (2015) proposed a functionally and anatomically refined framework, identifying two key subdivisions of PPS-related circuits in non-human primates (Figure 3). The first subsystem, conceptualized by the authors as primarily defensive, involves the parietal area VIP and premotor area F4 (Matelli & Luppino, 2001; Rizzolatti & Luppino, 2001). Area VIP specializes in the perception and spatial localization of nearby stimuli, while area F4 generates rapid reflex responses, such as defensive behaviours or obstacle avoidance. The second subsystem, comprising parietal areas AIP and 7b and premotor area F5, is more directly involved in action planning and execution. Notably, area F5 contains canonical neurons (Bonini et al., 2014) that have a visual selectivity for three-dimensional objects affording a specific hand-grasping configuration (Murata et al., 1997; Raos et al., 2006). The regions of this subsystem, characterized by sensory-tactile and hand-related properties, support visuomotor transformations essential for reaching and grasping. Their activity bridges perceptual encoding and motor output by

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transforming object features into motor programs appropriate for interaction in anticipation of contact, which contributes to the predictive encoding of action possibilities in PPS.

Collectively, authors reports the involvement of a broader frontoparietal circuit involving ventral premotor areas (PMv, areas F4, F5 and 6, Fogassi et al., 1992, 1996; Graziano et al., 1997; Rizzolatti et al., 1981), the posterior parietal cortex (PPC, areas 7a and 7b, Leinonen et al., 1979), the VIP (Avillac et al., 2007; Colby et al., 1993; Duhamel et al., 1998) and subcortical structures such as the putamen (Graziano & Gross, 1993).

# 1.2.3. Neural correlates of peripersonal space in humans

So far, identifying PPS-related networks in humans has proven more challenging than in non-human primates due to both anatomical differences between species and methodological limitations. Nonetheless, early theoretical accounts laid important groundwork for this distinction: as early as 1998, based on neuropsychological cases, Previc proposed that information within peripersonal space is primarily processed through the dorsal visual stream, including regions of the parietal cortex (Previc, 1998), a system traditionally associated with visually guided action (Goodale & Milner, 1992). In contrast, the ventral stream was posited to be more involved in processing far or extrapersonal information, supporting object perception and identification (Goodale & Milner, 1992). Following these initial proposals, and guided by analogies to primate models, studies involving both healthy participants and brain-damaged patients proposed putative homologues of the primate fronto-parietal circuit. These include mainly regions of the posterior parietal cortex (PPC), including the inferior and superior parietal lobules (IPL and SPL) and the intraparietal sulcus (IPS), as well as the ventral and dorsal parts of the PMC (Basile et al., 2024; Di Pellegrino & Làdavas, 2015; Grivaz et al., 2017; Sereno & Huang, 2006, 2014). On the whole,

parietal regions were found to consist of a core hub within this fronto-parietal network, with consistent activations of the postcentral gyrus, the SPL, the IPL, and the supramarginal gyrus (see Basile et al., 2024; Di Pellegrino & Làdavas, 2015; Grivaz et al., 2017 for reviews). In a narrative review, Basile et al. (2024) indeed underlined the role of the IPS as a key hub for processing peripersonal objects, facilitating dynamic spatial encoding and motor planning. In line with the somatotopic organization of PPS observed in monkeys, human studies report predominantly bilateral activations that vary depending on the body part involved. Although experimental manipulations mostly involve the right limbs, the right parietal cortex is frequently found to be specifically engaged, particularly in relation to its established role in spatial awareness and bodily representation (Azañón et al., 2010; Geers et al., 2021; Daprati et al., 2010).

In addition, premotor regions have been implicated in the early stages of action preparation and in complex sensorimotor processes (Avenanti et al., 2012; Makin et al., 2009; Serino et al., 2009). Specifically, the involvement of PMv in the sensory guidance of movement and in shaping effectors for effective specific movement (Binkofski et al., 1999; Davare et al., 2006; Ehrsson et al., 2000; Grèzes et al., 2003) aligns with its proposed homology to non-human primates' area F4 and F5 (Rizzolatti & Fabbri-Destro, 2010; Davare et al., 2008). In addition, evidence indicates that some PMv neurons in humans exhibit heightened responsiveness to looming stimuli (Cléry et al., 2017; Colby et al., 1993), which supports their involvement in initiating rapid behavioral reactions to potential threats. However, evidence for PMv recruitment in humans can be subtle as the response of premotor neurons tends to adapt rapidly to repeated visual stimulation (Makin et al., 2007; Rizzolatti et al., 1981c), and as finding activations in the PMv is highly task-dependent (Bartolo et al., 2014b; Grivaz et al., 2017). Specifically, stronger activation is generally observed

#### 1.2. Neural foundations of peripersonal space

during tasks involving overt motor execution, whereas its engagement is typically less consistent during passive observation of objects, or in motor imagery tasks (Grivaz et al., 2017).

The recruitment of this "core PPS network" composed of parietal and premotor regions (Basile et al., 2024) has been since completed through the engagement of other important structures depending on task demands. During visually guided reaching tasks, for example, activations in the parieto-occipital sulcus are often reported (dorsal, dPOS, and ventral, vPOS). These regions appear to contribute to visuomotor transformations necessary for directing actions toward targets in near space (Gallivan et al., 2009; Quinlan & Culham, 2007). Similarly, interaction with subcortical structures such as the cerebellum, long associated with motor processes (Grafton et al., 1996; Lotze et al., 1999) and more recently with multisensory integration (Blakemore et al., 1999, 2001; Schmahmann & Pandya, 1989; Schmahmann, 1996), is now believed to contribute to perceptual and motor processes in PPS (Bartolo et al., 2014b; Brozzoli et al., 2011; Coello & Delevoye-Turrell, 2007; Gentile et al., 2011). In tasks requiring the integration of multiple sensory signals, the temporo-parietal junction (TPJ) has also emerged as a potential contributor to PPS processing (Grivaz et al., 2017; Ionta et al., 2011). This region is often implicated in first-person perspective and self-location through multisensory integration, both of which are critical when representing space around the body.

To get a comprehensive understanding of information processing in PPS, Basile et al. (2024) proposed that the core PPS network co-activates with distributed networks based on the task and the context. For instance, it is often recruited along with a dorsal attention network (DAN), involved in spatial prioritization and goal-directed behaviours, and a ventral attention network (VAN), which contributes to the detection and redirection of attention toward behaviourally significant events (Figure 4). What appears from this proposition is that overall, PPS mechanisms

## 1.2.4. Linking brain mechanisms to behavioral evidence

in humans do not simply emerge from a restricted network. Instead, the fundamental PPS brain regions (which Basile calls "core region") interact with large-scale brain networks to combine bodily awareness with environmental and contextual information to guide adaptive behaviour.

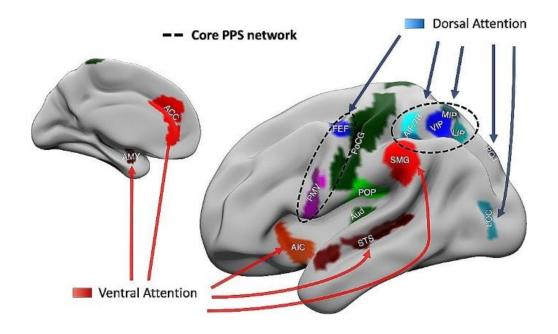


Figure 4. Rendered graphical representation of the core and extended PPS network. Core PPS areas are circled with dashed lines and composed of the ventral premotor cortex (PMV), frontal eye field in the dorsal premotor cortex (FEF), and anterior (AIP), ventral (VIP), medial (MIP), and lateral (LIP) divisions of the intraparietal sulcus. Regions are classified according to their involvement in large-scale networks (blue = dorsal attention network, red = ventral attention network, green = sensorimotor network). Reproduced from Basile et al. (2024).

## 1.2.4. Linking brain mechanisms to behavioral evidence

In parallel with neural and neurophysiological findings, clinical studies have revealed behavioral signatures of the specialized multisensory and sensorimotor processing that characterizes PPS. In particular, research on patients with unilateral brain lesions has made substantial contributions through the use of cross-modal extinction paradigms. These paradigms showed that the detection of a tactile stimulus on the contralesional side of the body (e.g., the left

## 1.2. Neural foundations of peripersonal space

hand following right-hemisphere damage) can be suppressed when a concurrent visual stimulus is presented near the ipsilesional side of the body (di Pellegrino et al., 1997; Farnè et al., 2000). This extinction effect occurs only when the visual stimulus is presented within the space immediately surrounding the body, which implies that this multisensory competition is constrained to PPS, and thus that PPS can be defined by its unique multisensory properties.

These patient-based evidences directly inspired the development of an experimental paradigm in healthy individuals, aimed at characterizing PPS representation and its underlying mechanisms through cross-modal (or multisensory) facilitation. In these paradigms, tactile detection tasks are combined with visual or auditory stimuli that are approaching the body. The presence of a stimulus looming toward the body leads to enhanced tactile processing, typically measured by faster reaction time (RT; Canzoneri et al., 2012; Noel et al., 2015; Serino et al., 2015). These paradigms aim to approximate the neural properties of PPS neurons, which integrate multisensory stimuli near the body and drive defensive and purposeful motor responses. Although these paradigms elegantly capture the specific effect of proximal stimuli in modulating the tactile processing and thus reflect the multisensory nature of the PPS, they fail to address its intrinsically motor component (de Vignemont & Farnè, 2024). That is, while these paradigms successfully index multisensory integration near the body, they are less informative about how PPS contributes to action planning and motor control. Therefore, alternative paradigms are needed to probe PPS within an interactive and action-oriented context.

One such approach involves reachability judgement tasks, built upon the action-oriented properties of PPS. Reachability-based and multisensory paradigms of PPS differ fundamentally in what they measure and the mechanisms they invoke. Indeed, reachability judgments directly index the content and the boundary of PPS as defined by one's actual or perceived action capabilities. In

this approach, participants estimate how far they can interact with objects with the hand or a tool, tapping into the same forward models and body-schema updates that support goal-directed actions (Coello et al., 2008; Geers & Coello, 2023, Submitted; Zanini et al., 2021). Reachability-based paradigms yield a stable, biomechanically grounded metric that flexibly adapts to changes in, for instance, posture or tool use, and ensures that PPS remains tightly coupled to the sensorimotor demands of the physical interaction (Geers & Coello, Submitted). In contrast, the aforementioned multisensory integration paradigm defines PPS by the distance at which looming visual or auditory stimuli speed tactile detection: tactile reaction times accelerate when an irrelevant stimulus approaches within a certain range of the body (Canzoneri et al., 2012; Serino et al., 2011). In such paradigm, the multisensory facilitation is usually computed as the gain in reaction time obtained in the multisensory condition (e.g., visual and tactile) compared to an unisensory condition (tactile only). While reaction time to tactile stimuli does improve when a looming stimulus approaches the body, the facilitation effect often extends beyond true reaching distance, often over 1 m from the body (Geers & Coello, 2023; Noel et al., 2020), and sometimes even up to 2.5m (Taffou & Viaud-Delmon, 2014). This stands in contrast to findings from single-cell studies in non-human primates, where distant peripersonal neurons typically respond only to stimuli within reachable space (Fogassi et al., 1999; Graziano et al., 1994; Rizzolatti et al., 1981c), which raises concerns about the specificity of this metric to a phenomenon usually restricted to action-relevant space, and by extension, the use of multisensory-based paradigms as a proxy for PPS boundary (Geers & Coello, 2023; Submitted).

Recent theoretical work supports this concern: in a comprehensive review, Geers and Coello (Submitted) argued that tactile facilitation induced by looming concurrent stimuli may be amplified by factors such as arousal, motor resonance, and contact anticipation. These confounding

#### 1.3. Peripersonal space as a sensorimotor interface

processes, while relevant to bodily vigilance and defensive mechanisms, are not strictly confined to PPS and may partly account for the extended spatial range observed in the facilitated detection of targets. In line with this observation, de Vignemont and Farnè (2024) suggest that such multisensory paradigm capture more defence-oriented aspect of PPS mechanisms, rather than those involved in action planning; for them, defensive and interactive properties of PPS may have co-evolved, but adapted paradigm should be developed to be able to properly disentangle their respective contribution to the observed behavioral effects.

Taken together, these considerations indicate that, given the present works on interaction with objects and the preparation for goal-directed action, the reachability-based framework offers a more functionally grounded approach. This framework grounds PPS mechanisms in the neurofunctional architecture of motor preparation, avoids confounds introduced by defensive and anticipatory processes, and provides an adaptable measure of space within which meaningful bodily interactions occur. For this reason, the experimental contribution of this thesis adopts a paradigm derived from classical reachability judgement tasks, which has been designed and proven for probing the sensorimotor dimension of PPS in contexts of voluntary action.

#### 1.3. PERIPERSONAL SPACE AS A SENSORIMOTOR INTERFACE

## 1.3.1. Body schema and action-relevant representations

The previous sections demonstrated that the identification of a core PPS network between premotor and parietal cortices showed that it was, by nature, a space grounded in the interacting body and fundamentally tailored for action. As proof, the identification of large-scale brain networks involved in PPS processing shows that PPS is not merely a passive perceptual construct but rather a functional and plastic interface for interaction between the body and the environment

(Basile et al., 2024; Bufacchi & Iannetti, 2018; Cléry et al., 2015; Di Pellegrino & Làdavas, 2015). Mechanisms such as the integration of multisensory and motor-related information in both retinal and body-centred reference frames thus contribute to defining the spatial boundaries of the body for interaction. PPS is thereby continuously reshaped to adapt to changes in bodily states and environmental demands. This conceptualization provides evidence for a direct connection with the construct of the body schema, an implicit, sensorimotor representation that governs movement execution and adapted interaction with the world (Holmes & Spence, 2004).

The notion of the *body schema* refers to a non-conscious, proprioceptive representation that encodes the spatial configuration of the body for motor aims (de Vignemont, 2010; Longo & Haggard, 2010). It should be noted that while alternative representation of the body have been proposed and could have been discussed here, such as the body model, storing the body's metrics properties (Longo & Haggard, 2010), or the postural and superficial schema, reflecting respectively the position of the body in space in relation to movement and the position of sensation on the body (Medina & Coslett, 2010), this thesis will adopt the term body schema to align with the terminology most commonly employed in the PPS literature, and to preserve narrative coherence. Crucially, unlike the body image, which involves an explicit awareness and subjective representation of one's bodily form and structure, the body schema operates implicitly, providing a continuously updated framework for action (Paillard, 1999). The body schema and PPS share notable functional parallels, both crucially involved in the preparation and execution of goaldirected action through dynamic adaptations. As a consequence of the overlapping of these two concepts, body schema and PPS are often similarly modulated in experimental contexts, which has led in the past to questions about their uniqueness (Cardinali et al., 2009). However, while the body schema ensures the coherent tracking of limb positions and configuration, PPS extends this

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representation into external space, defining an action-relevant zone in which objects and stimuli are processed as functionally significant entities. In essence, PPS can be understood as an extracorporeal extension of the body schema into the external world (Brozzoli et al., 2013; Makin et al., 2008). This perspective is supported by converging experimental and clinical evidence showing that PPS representation is flexible and that alterations in the body schema can induce corresponding shifts in its boundaries.

# 1.3.2. An adaptive body-centred remapping for action

One of the most compelling lines of evidence supporting the plasticity of PPS following modifications of the body schema comes from studies that studied the effect of modifications of effectors, either expanding or shrinking the possibility of acting on the environment. Notably, studies on limb immobilization revealed that restricting limb movement through transient immobilization is reflected through a diminished spatial accuracy of movement (Huber et al., 2006) and impaired coordination (Moisello et al., 2008). Bassolino et al. (2015) and Toussaint et al. (2020) further demonstrated that this modification of the sensorimotor representation of the body had a direct effect on PPS representation, as they observed a significant contraction of PPS following the immobilization period, suggesting that the brain continuously updates spatial representations based on motor capability. Notably, this updating process occurs rapidly: for instance, restraining an upper limb leads to a decrease in cortical excitability in the motor regions responsible for its control (Facchini et al., 2002) as soon as 10- or 12-hours following immobilization (Avanzino et al., 2011; Huber et al., 2006). In line with the adaptive purpose of this process, Canzoneri et al. found that it seemed to be reversible: indeed, following limb amputation, participants showed a reduction in the extent of their PPS representation, reflecting a recalibration of action possibilities. However, when these individuals were equipped with a

prosthesis, their PPS expanded, indicating that they functionally integrated their prosthesis into the body schema so that it partially replaced the missing limb.

Conversely, tool-use paradigms illustrate the capacity of PPS to expand in response to increased action possibilities. Seminal work by Iriki et al. (1996; Maravita & Iriki, 2004; see Figure 5) in non-human primates provided foundational evidence for this phenomenon. In their pioneering study, macaque monkeys were trained to use a rake to retrieve food placed beyond their natural reaching distance. Recordings from bimodal visuo-tactile neurons in the anterior part of the intraparietal sulcus revealed that, following active tool use, these neurons extended their receptive fields to effectively incorporate the tool as an extension of the body. Notably, this plasticity was contingent upon active tool manipulation, as passive holding of the tool did not elicit similar changes.

In human studies, Cardinali et al. (2009) provided the first empirical evidence consistent with an increase in the representation of arm length following tool use. In this study, the authors assessed participants' free-hand kinematics before and after active tool use. Notably, after tool use, participants exhibited increased movement latencies and a reduced peak amplitude in their reaching movements, resulting in an overall prolongation of movement times, consistent with an expanded representation of arm length (i.e., a decreased distance to reach the target). Since additional research has corroborated these findings, demonstrating that individuals who regularly use handheld tools exhibit an expanded PPS representations that encompass the functional range of the tool (Cardinali et al., 2009; Canzoneri et al., 2012; Farnè & Làdavas, 2000; Longo & Lourenco, 2006; Sposito et al., 2012). It is however interesting to note that this plasticity of PPS appears to be contingent on the intention to act: Witt et al. (2005) indeed demonstrated that when participants held a tool with the intention to use it, their perceived PPS boundary expanded.

## 1.3. Peripersonal space as a sensorimotor interface

However, when participants held the same tool without the intention to reach an object, their perceived PPS boundary remained unchanged.

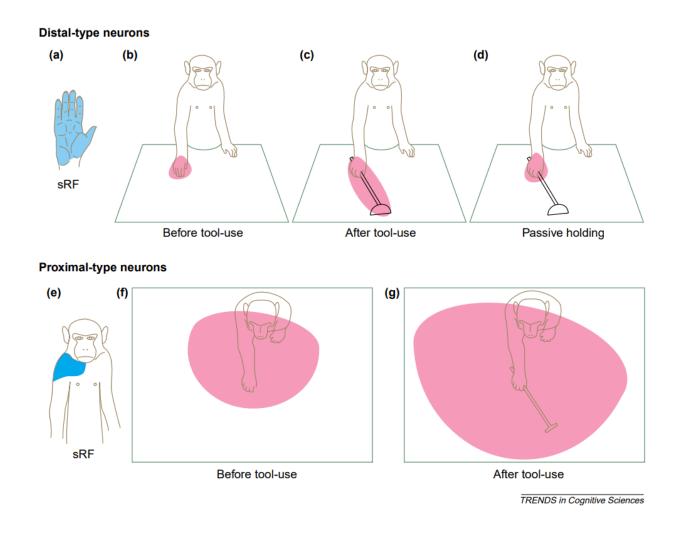


Figure 5. Changes in bimodal receptive fields (RF) properties following tool use. Somatosensory RFs (sRF; blue) were defined by the authors by light touch, joint manipulation, or active hand use; visual RFs (vRF; pink) by response to visual probes. (a) Distal sRF and vRF were represented (b) before tool use, (c) immediately after tool use, and (d) during passive holding of the tool. (e) Proximal sRF and vRF represented (f) before and (g) after tool use. Reproduced from Maravita & Iriki (2004).

One proposed mechanism underlying the plasticity of PPS involves the reorganization of multisensory receptive fields. Under normal conditions, the extent of PPS is determined by the extent of visuo-tactile receptive fields in the frontoparietal network. However, experimental

## 1.3.3. A contextual modulation driven by environmental factors

manipulations, particularly those involving synchronous visuo-tactile stimulation, can significantly alter this representation through perceptual illusions (Botvinick & Cohen, 1998). For instance, work by Blanke et al. (2015) demonstrated that bodily illusions, such as the rubber hand illusion or full-body ownership manipulations in virtual reality, can lead to a measurable expansion of PPS of the participant, incorporating artificial or virtual body parts into the self-representation.

Beyond the modulation of PPS through direct changes to the body schema, interesting evidence for the dynamic nature of PPS also comes from neuropsychological observations, particularly in hemi-spatial neglect. Hemi-spatial neglect is typically characterized as a deficit in spatial awareness contralateral to a brain lesion, often involving right parietal regions (Heilman & Valenstein, 1979) several studies have shown that this neglect can selectively affect either peripersonal or extrapersonal space, which again support a functional dissociation between these spatial domains. For instance, in cases of right parietal damage, patients may exhibit neglect restricted to the space immediately surrounding the body. Remarkably, the spatial extent of their symptoms extends following tool use as if, as formulated by Berti and Frassinetti (2000), "far becomes near" (see also Beschin & Robertson, 1997; Halligan et al., 2003). Reversely, tool use has been shown to partially restore awareness of the neglected space in patient showing extrapersonal neglect, suggesting that the expansion of PPS through action can compensate for deficits in spatial representation (Farnè et al., 2005).

## 1.3.3. A contextual modulation driven by environmental factors

The flexibility of PPS and its tight link with body schema aligns closely with theories of embodied cognition, which posits that cognitive processes are deeply rooted in the body's interactions with the environment (Barsalou, 1999; Glenberg, 2010). Within this framework, PPS

#### 1.3. Peripersonal space as a sensorimotor interface

is inevitably influenced by the disposition of the body in the environment and can be recalibrated as a function of its motor capacities. However, interaction is inherently a dyadic process, and require the involvement of another interactant. In other words, the cognitive processes at stake in PPS mechanism must take into account not only the characteristic of their internal and bodily state, but also the characteristics of the external environment.

In the continuity of this reflection, a long-lasting debate has centred on the primary function of PPS, with some authors proposing that PPS mechanisms are fundamentally recruited for appetitive, goal-directed interactions, what has been referred to as the *Plan A* for instrumental behaviour (de Vignemont & Farnè, 2024). As such, interaction with objects is one of the primary functions of PPS, and PPS mechanisms are proposed to be quasi-systematically recruited in appetitive action planning. If PPS serves as a functional interface between the body and nearby objects, it must therefore adapt not only to the body of the agent performing the action, but also to the entity considered for interaction. For instance, PPS is extended in the presence of appetitive objects (Bertonatti et al., 2021; Coello et al., 2018; Valdés-Conroy et al., 2012), as if it extended to facilitate action toward appetitive objects.

Because PPS defines the space near the body, it is not only a zone for potential interaction, but also one that requires regulation to ensure safety, in which PPS has been this time proposed as a *Plan B* for protective behaviour (de Vignemont & Farnè, 2024). Neurophysiological studies indeed showed that threatening stimuli in close proximity of the body elicit defensive behaviours, such as withdrawal or flinching, when they enter the peripersonal zone (Cooke & Graziano, 2003; Graziano et al., 2002). Thus, some objects must be kept at a distance rather than incorporated into PPS, and therefore triggers specific adaptation in PPS. For instance, the presence of static aversive stimuli near the body leads to a contraction of PPS boundaries reflecting a defensive mechanism

#### 1.4.1. Space as a social tool for protective purposes

that limits exposure to danger (Coello et al., 2012; Mustile et al., 2021, Valdés-Conroy, et al., 2012). Overall, PPS functions as a dynamic buffer zone between the body and the environment, and is consequently shaped by both internal states and external factors, whether they invite approach or necessitate avoidance.

## 1.4. THE SOCIAL AND INTERACTIVE DIMENSIONS OF PERIPERSONAL SPACE

# 1.4.1. Space as a social tool for protective purposes

A direct extension of its protective role, PPS functions as a spatial buffer that contributes to the regulation of social interactions (Coello & Cartaud, 2021). This social function supports a balance between approaching others closely enough to enable engagement; while maintaining sufficient distance to avoid their intrusion of one's PPS. When these implicit social norms are violated, such as through unexpected proximity, individuals often experience discomfort or initiate defensive reactions (Kennedy et al., 2009). In everyday interactions, people intuitively respect these personal boundaries in order to ensure smooth navigation and reduce the risk of conflicts.

Drawing on the ethological framework of proxemics (Hall, 1966), Coello and Cartaud proposed a model suggesting that the optimal distance for interpersonal communication, the interpersonal distance (IPD), was dynamically shaped from PPS boundaries. In this view, authors argue that PPS represents a "no-go zone" in regards to its protective role for the body. The IPD would thus be constructed around this buffer zone to maintain homeostasis. As an evidence, physiological responses to social intrusion into PPS have been shown to predict the preferred IPD for social interaction (Cartaud et al., 2018). According to this model, the preferred IPD emerges from the combination of two factors: the individual's current representation of PPS and the perceived threat (or, more broadly, the affective valence) of the social stimulus. The integration of

#### 1.4. The social and interactive dimensions of peripersonal space

these two dimensions helps determine the spatial limits individuals are willing to tolerate in a given social context. In sum, Coello and Cartaud argue that IPD is defined by the relationship linking spatialization to physiological homeostasis. This interplay between approach and avoidance, or between protection and engagement, reinforces the fact PPS is not only involved in mediating defensive responses, but also in spatially structuring social interactions.

Evidence from non-human primate highlighted the adaptability of PPS in social contexts. In a study by Fujii et al. (2007), when two monkeys were positioned closely such that their PPS overlapped, and a piece of food was placed at the intersection of their spaces, parietal activity related to reaching in PPS was reduced in the subordinate monkey. This reduced activation was accompanied by behavioral inhibition; however, neither behavioral nor neural inhibition was observed in the dominant monkey. Subsequent studies from the same team also revealed a shift in the prefrontal cortex activity in response to spatial competition: while PFC activity increased in the dominant monkey, it decreased in the subordinate one, illustrating hierarchical modulation of PPS-related processing (Fujii et al., 2009).

Human studies confirmed a mutual respect for each other's PPS. Coello et al. (2018) showed that in a cooperative token-selection task where two individuals were seated face-to-face in close proximity, individuals reduced their movement amplitude, as if they were splitting the action space between them. While this division appeared to constrain the area functionally exploited by each participant, the authors observed an expansion of PPS representation following the cooperative interaction, as if each participant's PPS expanded to encompass the other's action space in a collaborative task.

# 1.4.2. Space as a social tool for collaborative purpose

As a whole, the available evidence suggests that, in a social context, PPS has modular roles in structuring interactions with others: one's own PPS can be used as an individual landmark to prevent intrusion, and the inferred boundaries of others' PPS can guide social behaviour and help avoid conflict. However, this evidence also shows that PPS representation can extend to encompass that of another person following a collaborative task (Coello et al., 2018; Gigliotti et al., 2021), forming a "common peripersonal space". Investigating the cognitive basis of this phenomenon, Ruggiero et al. (2021) observed that the representation of another individual's PPS is influenced not only by physical proximity, but also by the ability of others to move their arms: this suggests that the representation of others' PPS may be related to the projection of one's own PPS. In parallel, Maister et al. (2015) observed that, after a shared sensory experience, participants experienced faster detection time with stimuli approaching a confederate's body, suggesting the creation of a shared sensory space. However, this effect did not bridge the physical space between the two individuals and remained confined to the area immediately surrounding their respective bodies. Rather than an expansion of PPS, the authors interpreted this as a partial remapping of the confederate's PPS onto the participant's own spatial representation. This interpretation was supported by evidence from Fossataro et al. (2016), who found that the hand-blink reflex, a defensive response typically associated with intrusions into PPS, could be elicited when witnessing an intrusion into others' PPS. Taken together, these results go in the direction of the emergence of a shared PPS representation between the agents under specific social and task conditions. The growing body of evidence corroborates the fact that PPS mechanisms are central in the understanding of others' intentions (Bogdanova et al., 2021; Kilner et al., 2004), as they may integrate information about the bodies of others. These effects are of particular importance during

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joint action, where individuals coordinate their movements within a shared spatial framework, a "supraindividual representation of space" (Gigliotti et al., 2021; see also Cardellicchio et al., 2013; Sacheli et al., 2013). As evidence, Cardellicchio et al. (2013) showed that motor facilitation, reflected by corticospinal excitability, occurred not only when objects were within the participant's own reach but also when they were located in another individual's reachable space. They interpreted this as evidence that the observer's motor system can encode action-relevant affordances in the peripersonal space of others, possibly subtending coordination in social interaction.

From a neurocognitive perspective, monkey and human studies have long demonstrated that populations of neurons in the ventral part of the premotor and parietal cortices (Rizzolatti & Craighero, 2004; Kilner et al., 2009; Caggiano et al., 2009), often referred to as *mirror neurons*, respond to both executed and observed actions. It has been proposed that this system could be involved in the construction of a body-centred representation of others, analogous to one's own. This hypothesis is supported by findings demonstrating that certain neuronal populations in the parietal (Ishida et al., 2010) and premotor ventral (Brozzoli et al., 2013) cortices encode the space surrounding both the self and others, suggesting a partially shared spatial coding mechanism.

## 1.4.3. Conclusion: interacting through and beyond physical properties

In sum, the evidences reviewed thus far indicate that the functions of PPS extend beyond that of a passive safety buffer. PPS subserves both defensive and approach-related functions: it is a multisensory interface rooted in the sensorimotor system that simultaneously represents a safety boundary around the body and acts as a prioritized interface for goal-directed action within the environment. To fulfil these complementary roles, PPS adapts to the characteristics of both

## 1.4.3. Conclusion: interacting through and beyond physical properties

interacting parties: the agent's body and the external stimuli. When the interaction involves other individuals, the distinction between one's own and others' spaces is shaped by social cues, contextual demands, and the nature of the interpersonal interaction. When the interaction involves objects, the extent of PPS and the processing of those objects are modulated according to their properties, relevance, and contextual meaning. Crucially, not all objects are processed equally: some are not merely physical entities but carry a social value. This convergence raises critical questions: for instance, how does PPS accommodate external stimuli that are socially meaningful, such as those to which ownership is attributed? In the next section, I will examine how object ownership constitutes a distinctive cue that imbues objects with special value by carrying simultaneously self and social relevance.

## 2.1. The concept of ownership: from law to cognition

# 2. What is mine, what is yours

#### 2.1. THE CONCEPT OF OWNERSHIP: FROM LAW TO COGNITION

## 2.1.1. Ownership as a social construct: objects, others, and society

Object ownership, that is the sense that a particular object "belongs" to a person, is a pervasive social construct that structures human interaction and cognition (Pierce et al., 2001). From early in development, children acquire and enforce intuitive ownership norms through observing social exchanges and conflicts over possession: by age two, toddlers reliably use possessive language ("mine") and resist peers' attempts to take their toys, and by age three to four they distinguish legitimate transfers (gifts) from illegitimate ones (theft) (Brownell et al., 2013; Friedman & Neary, 2008; Nancekivell & Friedman, 2014). These norms are systematically codified in language through possessive pronouns and affiliation terms, in moral expectations for respecting others' property, and in legal systems that formalise rights and obligations (Hay, 2006; Rochat et al., 2014). From a phylogenetical perspective, comparative evidence further indicates that respect for ownership (or for, at least, a precursory bond between an item and an individual) arises across species without formal enforcement: evolutionary models show that bourgeois equilibria (where challengers respect an owner's claim) emerge quasi-systematically in nature, making owners more willing to defend resources, while anti-bourgeois behaviour (the respect for the absence of ownership of an object) is unstable and rarely observed (Sherratt & Mesterton-Gibbons, 2015). Because, virtually, every object in social environments is assumed to have an owner, and because owning an object does make sense only if its ownership is mutually recognised and respected among persons, ownership must be conceived as a triadic relation involving self, other, and object rather than a simple self-object dyad (Pierce et al., 2001). Thus, implicit social norms regarding ownership are often automatically respected to reduce the risk of social conflict. In addition, as

ownership is not always clearly stated, it is often inferred from social cues, such as perceived control over an object (e.g., observing who handles or uses it, Pierce et al., 2001), physical proximity (Scorolli et al., 2018), temporal priority (who encountered the object first, Friedman & Neary, 2008; Scorolli et al., 2018), or even personal investment (who has invested effort or resources into the object, Pierce et al., 2001).

In line with its role as a cue subserving smooth social interaction, modern accounts distinguish legal from psychological ownership. Legal ownership refers to formal property rights under law (Morewedge, 2021), whereas psychological ownership refers to the personal sense that something belongs to oneself, that is, the feeling that a thing is *mine*. Morewedge (2021) thus proposed that psychological ownership usually tracks legal title, but the two can diverge: one may feel ownership of a borrowed item even without legal claim, or conversely own an unused asset without feeling attached to it. In his narrative review, Morewedge proposes a dual-process model of ownership; antecedents' events (e.g., repeated use, creation, cues of control) form implicit self-object associations, leading to an automatic inference of ownership, which can then be consciously endorsed, corrected, or rejected. This model explains that ownership exists on a continuum of selfobject relations, from mere legal possession to fully internalized identification. For instance, people may use and feel ownership for objects they do not legally own, or legally own objects they do not use or feel ownership for. In other words, ownership is a "how", i.e., a rule-governed attribution, and also a "what", i.e., a feeling of special relation to certain objects. In this view, ownership is not a binary property, but varies in intensity and psychological immediacy by integrating property rights and intangible self-relations.

## 2.1. The concept of ownership: from law to cognition

# 2.1.2. The link between ownership and the self

Morewedge's model shows that beyond being a social information pointing one's right over possessions, ownership is also fundamentally tied to the self. In fact, prior to being theorized as a social concept, the notion of ownership has long been linked with the self. More than one century ago, James (1890) already suggested that "a man's Self is the sum total of all that they can call his", explicitly including not only his body and mind, but also his clothes, home, possessions, and family, as he introduced the idea of the *material self*: the set of physical possessions and body parts over which one feels personal control. Likewise, Jean-Paul Sartre (1943) noted that people often experience ownership as a self-like extension: one might say "the totality of my possessions reflects the totality of my being [...] I am what I have [...] What is mine is myself". These propositions anchor the roots of possession in the self-concept, a perspective that contemporary theorists continue to share: for example, in consumer psychology, Belk (1988) argued that people regard certain possessions as literal parts of their identity by theorizing the notion of the extended self. In his opinion paper, he posits that the self is embodied and extend through "material things" ranging from clothing and vehicles to pets or digital avatars, functioning as a symbolic and functional extensions of who one is. Going even further, he states that possessions do not merely reflect identity, but actively constitute it: they are integrated into the self-concept through processes such as control, personalization, habitual use, and emotional attachment. Together, these perspectives situate ownership not merely as a legal social status but as a psychological relationship that imbues objects with self-relevance: it is the subjective sense of "mine-ness" of things that integrates objects into the notion of self.

#### 2.2.1. Self-prioritization and cognitive benefits of ownership

#### 2.2. OBJECT AND THE SELF: COGNITIVE AND NEURAL MECHANISMS

# 2.2.1. Self-prioritization and cognitive benefits of ownership

Ownership thus represents a powerful bond between owners and their objects, initiating a form of self-relevance for the owned objects. Thus, to avoid social conflict and to enable rapid and efficient interactions with our belongings among the large quantity of information constituting our environment, it is not surprising that we advantage self-relevant information and items during information processing, and that self-relevance is, as a general rule, held to guide our cognition and action. Following this idea, self-relevance affords benefits during both thinking and acting (Baumeister, 2023), a phenomenon often termed as self-prioritization (or, when referring to memory, self-reference effect, SRE). This self-prioritization illustrates the fact that stimuli (sometimes arbitrarily) labelled as "me" or "mine" are usually processed faster and remembered better than identical items labelled as associated or belonging to others. For instance, in a shapelabel matching task, Sui et al. (2012) asked participants to learn the association between shapes and individuals (e.g., circle = Self, square = Friend, triangle = Stranger) before judging shape-label pairs. Responses were consistently faster and more accurate for shapes designated as "Self", which was interpreted as a general self-related bias: things that are related to oneself capture attention and mnemonic resources more readily. Similar findings were observed in object-categorization tasks: after learning associations between individuals and objects (e.g., oneself owns pens, and a stranger owns pencils), participants were faster to indicate to whom objects from each class of items belong (Golubickis et al., 2018, 2021). Overall, self-prioritization, proposed to consist of a preferential processing of any self-relevant information, has been extensively demonstrated to bias cognitive processes (see Cunningham & Turk, 2017, for an extensive review of self-processing bias).

#### 2.2. Object and the self: cognitive and neural mechanisms

In an attempt to account for these various biases, Humphreys and Sui (2016) proposed the Self-Attention Network (SAN) model. The SAN posits that self-relevant stimuli benefit from automatic and perception-based prioritization (Humphreys & Sui, 2016; Sui & Humphreys, 2015, 2017). Authors posit that this prioritization takes its root through attentional mechanisms relying on the vmPFC, an amodal self-relevance hub, that interacts with two circuits: (I) a top-down circuit underlying attentional control and involving the dorsolateral prefrontal cortex (dlPFC), and (II) a bottom-up circuit underlying attention-orienting mechanisms and involving the pSTS. As a consequence, when the vmPFC signals the self-relevance of a material, even an arbitrary or inconsequential one, the saliency of the said material is proposed to be enhanced through an interplay of top-down and bottom-up attentional mechanisms.

# 2.2.2. Neural correlates of self-relevance

Before the SAN, early functional neuroimaging studies already investigated the neural signature of self-relevant processing. For instance, Kelley et al. (2002) found that making trait judgements about oneself selectively engaged a region of the mPFC. From this finding, a series of studies consistently reported the activation of medial regions, including mPFC, anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), and precuneus, when individuals process self-relevant information such as one's face, name, autobiographical facts or objects (Kim & Johnson, 2012; Platek & Kemp, 2009; Uddin et al., 2005). Northoff and Bermpohl (2004) coined these areas cortical midline structures (CMS), and proposed that they form a "model of the self" with subregions supporting self-representation, evaluation, and the global integration of self-relevant stimuli. A comprehensive meta-analysis performed by the same team confirmed that all self-related tasks robustly engaged the CMS across diverse functional domains (verbal, spatial, emotional, Northoff et al., 2006). The authors concluded that self-referential processing in CMS constituted

#### 2.2.2. Neural correlates of self-relevance

the "core of our self" and reflected a fundamental neural substrate underlying the unification of various concepts around the self in the brain.

Interestingly, these midline structures are key components of a larger system known as the default mode network (DMN), whose core is primarily composed of the mPFC, the PCC, and the inferior parietal lobule (IPL). This network was first discussed by Raichle et al. (2001) as a set of regions more active at rest than during externally directed tasks, and was later synthesized as a coherent anatomical system underpinning a range of self-relevant thoughts such as autobiographical memory, self-referential evaluation, and the imagination of social interactions (Buckner et al., 2008). Converging evidence from resting-state parcellation demonstrated that most DMN regions also contribute to social cognition, including, most notably, the mPFC, TPJ, and pSTS (Mars et al., 2012). These regions are often recruited during mentalization, perspectivetaking, interpersonal coordination, and, more generally, processes involved in social cognition (Li et al., 2014; Mars et al., 2012). Further meta-analytical work confirmed that tasks involving selfother distinction coactivate these overlapping regions, which underscore a shared representational architecture for processing both self- and other-related information and representations (Schilbach et al., 2008). The overlap of self- and other-related activations within these different networks raises theoretical questions about the organizational principles of social cognition and the role of the self in cognition. Indeed, this functional overlap raises the question of whether a shared representational mechanism (or representational continuum) processes both self- and otherrelevant information, suggesting that these regions contribute to both self-representation and social cognition.

Specifically, among these networks known to subserve self-processing, vmPFC has often been designated as a hub subtending the processing of self-relevant content (Sui & Humphreys, 2015;

## 2.2. Object and the self: cognitive and neural mechanisms

Wagner et al., 2012). Indeed, activation in this structure correlates with the personal significance of the material: stimuli or traits judged as more personally important elicit stronger vmPFC activation, whereas increasing psychological distance for the self is associated with attenuated vmPFC responses (D'Argembeau, 2013). This pattern aligns with theoretical models that conceive the vmPFC as a central self-representation hub that assigns elevated salience or value to information tagged as self-relevant, such as, for example, the SAN (Humphreys & Sui, 2016). Some meta-analytic reviews even support a ventral-dorsal gradient in mPFC, with the ventral mPFC preferentially engaged by self-related judgement and the dorsal mPFC by other-related judgement (D'Argembeau, 2013, Denny et al., 2012). This division was alternatively interpreted in terms of functional specialization, with the vmPFC playing a key role in a more affective or motivational valuation of (self-relevant) stimuli (García et al., 2015; Roy et al., 2012; see Lieberman et al., 2019 for a review), while the dmPFC was proposed to be implicated in more higher-order social processes such as self-other separation (Wittmann et al., 2021), and in tracking the relative social value of information for self and others (Piva et al., 2019; Su et al., 2025; Tomova et al., 2020).

## 2.2.3. Neural correlates of object ownership

Importantly, the implication of these neural structures extends from abstract self-referential information to self-owned objects: for instance, Turk et al. (2011) showed that the activity of the vmPFC and dmPFC was selectively modulated by object ownership, with the dmPFC being specifically engaged in the processing of self-owned objects, in line with its role in tracking socially relevant information (Su et al., 2025). Similarly, Kim and Johnson (2012) proposed that the preferential activation of the mPFC is evidence for the incorporation of self-owned objects into an *extended self*, that is, the incorporation of stimuli into one's own representation of the self (Belk,

1988; Beggan, 1992), interestingly echoing Sartre's seminal proposition (1943). Supporting this framework, Lockwood et al. (2018) showed that vmPFC and anterior cingulate cortex sulcus (ACCs) responded more strongly (although not specifically) to self-owned associations compared to those associated with friends or strangers, while the adjacent anterior cingulate gyrus (ACCg) coded ownership associations for others. Altogether, these findings point to a distributed network in which core midline regions integrate self-relevant information through an affective and social prism. Nonetheless, the neural correlates of object ownership remain yet underexplored. To date, only a handful of neuroimaging studies have directly contrasted self- and other-owned objects, and most paradigms have not disambiguated ownership-related activations from those driven by mere semantic valuation or task-related instructional effects.

## 2.2.4. Challenges to the specificity of the self-bias: a contextual modulation

Despite the above findings, recent work has questioned whether any brain area, particularly the vmPFC, is uniquely dedicated to self-processing. Critics argue that vmPFC is not a specialized "self-hub", as such a node would lack neurofunctional specificity (García et al., 2015; Golubickis & Macrae, 2023), especially as the vmPFC is known to be actively engaged across a wide range of tasks (e.g., decision making, emotion regulation and affective processing, Hiser & Koenigs, 2018; Lopez-Gamundi et al., 2021; Pessoa, 2008) and that the literature lacks consistency about its specific and systematic involvement in the processing of self-relevant information (Lieberman et al., 2019). Its engagement may rather reflect general cognitive function rather than the nonspecific saliency of any self-relevant information. Further advocating against the specificity of the vmPFC in self-relevant encoding, some authors found that this structure is involved in the processing of both self- and other-relevant information, with differential activation reflecting more a quantitative rather than qualitative difference in processing (Tacikowski et al., 2010). Supporting

## 2.2. Object and the self: cognitive and neural mechanisms

this interpretation, several studies have shown that temporary lesion of the vmPFC fails to consistently abolish self-prioritization effects (e.g., Schäfer & Frings, 2019). This suggests that while regions like the vmPFC may contribute to the processing of self-relevant information, they are not strictly necessary for the emergence of self-bias.

In line with this view and in an effort to clarify the neurocognitive basis of self-processing, Moran et al. (2013) proposed three models centred on the role of the mPFC in self-related cognition (Figure 6). The first account suggests that self-related processing relies on general social mechanisms, implying that processing self-related information engages the same neural systems involved in thinking about others, making the self a "powerful-but-ordinary case of social processing". A second account based on a proposition made by Heatherton (2011) conceptualizes the mPFC as a convergence hub that integrates complex and multimodal information from secondary sensory areas to form a unified representational space, leading to a form of conscious access to a "workspace" that social and self-related thoughts would particularly recruit. The third model proposes that the mPFC operates as a "meta-cognitive controller" that guides internally directed cognition and attentional focus time after time, a process naturally oriented toward thinking about our own self and our social network. Shortly after this theoretical reflection, metaanalytic evidence (de la Vega et al., 2016; Lieberman et al., 2019) revealed that the medial frontal cortex does not indeed fractionate neatly into self-only versus other-only modules; rather, individual medial frontal regions subregions show mixed associations with many psychological functions, including processing social information, but that no area was exclusively activated by self-related concept.

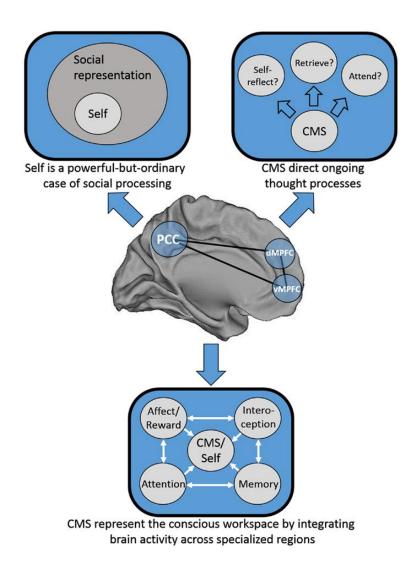


Figure 6. Schematic representation of the three possible models of CMS function. Reproduced from Moran et al. (2013).

The foregoing perspective thus supports a distributed network account of self-processing, rather than a dedicated self-hub. However, this view raises a question: how can the well-documented self-prioritization emerge in the absence of a specialized self-processing hub? Golubickis and Macrae (2023) argue that self-prioritization is, similarly to the recruitment of a self-network, not unique, but arises from the interaction of general attentional, executive, and memory networks. This view indicates that self-associated stimuli are not privileged because they are processed by a specialized self-module, but because they benefit from rapid associative

encoding and enhanced salience within domain-general systems. From this contextual perspective, self-prioritization is not a fixed or automatic outcome but one that is modulated by various factors, including the context, the instructions, and the relevance of the self-related information for the task and individuals (Caughey et al., 2021; Falbén et al., 2020; Golubickis & Macrae, 2023), as well as by factors such as the valence of the stimulus (Golubickis et al., 2021; Pereira et al., 2019, 2021) or the conformity to participants' identity (Falbén et al., 2020). Proponents of this view thus underline the fact that the manifestation of self-bias varies systematically with experiment context, and that these multiple manifestations do not correlates together, indicating the existence of distinct self-biases (Nijhof et al., 2020).

Efforts to isolate of self-specific neural and behavioral signatures or understand their nature have been hindered by persistent methodological limitations inherent in the design of current paradigm and the nature of the stimuli employed. Common paradigms used to demonstrate a self-prioritization are the shape-label tasks (where participants first learn arbitrary associations between geometric shapes and social labels, typically "self", "friend", and "stranger", and are then asked to verify whether subsequently presented shape-label pairings match the learned associations, Sui et al., 2012), the classification tasks (where participants categorize stimuli such as words, images, or objects according to their association with the self or others, Cunningham et al., 2008; Symons & Johnson, 1997) or tasks comparing own-name and other-name (Moray, 1959; Shapiro et al., 1997; Yang et al., 2013). However, the effects found in such paradigms may be driven by different confounding factors. For instance, naming tasks may be explained by general psycholinguistic confounds (García et al., 2015), which raises questions about the familiarity and the frequency of the stimuli. Besides, shape-label tasks or classification tasks suffer from methodological drawbacks: these paradigms are indeed heavily reliant on explicit self-other associations

## 2.3.1. The situated nature of ownership effects

established during the task itself, and participants are most often instructed to perform a task directly and explicitly involving the self-relevant information. As Golubickis and Macrae (2023) caution, such methods may confound true stimulus-driven prioritization with top-down, instruction-driven performance. Without disentangling these influences, it remains unclear to what extent self-prioritization reflects an intrinsic processing advantage for self-related stimuli as opposed to a contextual amplification shaped by task structure and expectation.

# 2.3. HOW ARE OBJECTS PRIORITIZED? OWNERSHIP AS A CONTEXTUAL CUE FOR SELF-RELEVANCE IN ACTION

# 2.3.1. The situated nature of ownership effects

In the previous section, I discussed how ownership and self-relevance were tightly linked. Given that ownership inherently entails a self-referential component, I explored the behavioral consequences of prioritizing self-related information within a social context. This discussion addressed both general categories of stimuli and object-specific processes, with a particular consideration of the neurocognitive mechanisms supporting this self-processing bias. I reviewed two different propositions of the literature: one postulating an automatic and general self-prioritization of self-related information, and one positing a situation-dependent prioritization of relevant information subtended by the recruitment of distributed networks. If the latter account holds, then, one may infer that the prioritized processing of self-relevant objects such as self-owned objects would be contingent on contextual factors such as spatial accessibility, and would manifest most robustly when these objects are located within PPS, where interaction is possible and socially appropriate.

Indeed, although the self-relevance effect is a broad term and may refer to various content, it is crucial to consider the specificity of objects as targets for interaction. Unlike abstract self-related

#### 2.3. How are objects prioritized? Ownership as a contextual cue for self-relevance in action

stimuli such as names or shapes, objects inherently afford action-related properties: they invite action of the body. To try to account for the attentional prioritization that could arise from the processing of objects through ownership, Truong and Todd (2017) proposed the Self as Ownership in Attention Prioritization (SOAP), an innovative account of how ownership contributes to selfrelevance by distinguishing between two conceptualizations of the self: the "self-as-subject", and the "self-as-object". In their model, the self-as-subject refers to the agentive, first-person perspective that underly volitional action, whereas the self-as-object designates the self as a stimulus that can become salient during cognitive evaluation, like an external item or stimulus (Figure 7). According to this framework, ownership amplifies the attentional salience of an object by both making it stand out as part of the self's representation, corresponding to a typical selfprioritization effect, but also by assigning motivational value to it, as it becomes relevant for goal pursuit. However, this framework remains intentionally primarily anchored in representational and attentional processes. It accounts for why owned objects may stand out as salient, but intentionally overlooks how such objects are embedded within the embodied and action-oriented nature of the agent-object interaction. Indeed, unlike abstract symbols of the self (e.g., one's name or the association with a shape), objects invite and constrain action in a way that is inherently sensorimotor. As such, considering only the tag for attentional and motivational relevance constituted by object ownership may be a reductive account of the prioritization of objects in interaction. Rather, the perspective of ownership as an embodied cue that moderates the perceived

#### 2.3.2. Ownership and sensorimotor coding in peripersonal space

affordances of objects would be worth considering further, particularly when these objects are situated in the action-oriented PPS.

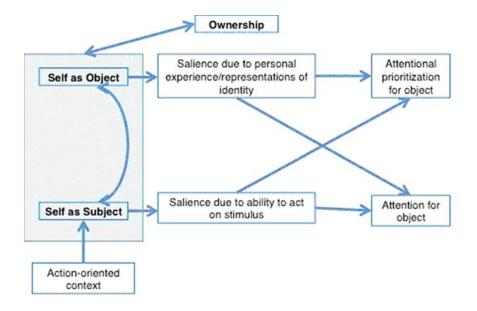


Figure 7. Schematic representation of the SOAP framework. Object ownership increases attentional salience via two routes: self-as-object, where salience arises through associations with identity and personal relevance, and self-as-subject, where salience arises through motivational processes associated with actions permitted by ownership. Authors propose that the brain network associated with both routes overlaps with the network mediating affective and motivational modulation of attention in order to prioritize the most relevant stimuli depending on the context. Reproduced from Truong & Todd (2017).

# 2.3.2. Ownership and sensorimotor coding in peripersonal space

Within everyday interactions, the potential for interaction of objects is not uniformly distributed across space: only objects located within one's PPS can be acted upon directly. Then, when an object is self-owned, it may benefit from a specific processing, not just because it is tagged as "mine", but also because it becomes a likely candidate for action. This is particularly important in social settings, where the distinction between what is mine and what is yours regulates appropriate interaction. In this context, one might predict a specific prioritization of owned objects

## 2.3. How are objects prioritized? Ownership as a contextual cue for self-relevance in action

within PPS: here, ownership does not merely label an object as self-related but also modulates its affordance by signalling that it is both relevant and permissible to act upon.

Object ownership seems thus to be crucial in the selection of targets for motor actions (Constable et al., 2011, 2019; Desebrock et al., 2018). As evidence, in a task requiring participants to grasp and lift a mug, Constable et al. (2011) showed that participants put less force and acceleration in movements directed toward other-referenced objects, as if they cared more for the objects belonging to others. This effect was observed in adults and children as early as 2 years of age (Kritikos et al., 2020). Moreover, Constable et al. (2011) reported a spatial compatibility effect between the orientation of the handle of a mug and the location of the response key used to respond to a stimulus presented on the mug handle, although the effect was observed only when the mug was the participant's own mug. The authors proposed that the availability of certain affordances can be altered by the (absence of) authorization to act granted by ownership, "as if the action system is blind to the potential for action toward another person's property" (Constable et al., 2011). Overall, these data support the fact that object ownership may be embodied within the sensorimotor system (Blakemore & Frith, 2003), enriching thus the concept of affordances generally used to account for the fact that objects' features automatically potentiate motor components of the action they afford (Phillips & Ward, 2002; Tucker & Ellis, 1998). The results of Constable et al. (2011) also suggest that the self can be extended beyond the body itself to encompass idiosyncratic experiences of objects (James, 1890), thus imposing the distinction items that are relevant for oneself from those that are not.

#### 2.3.2. Ownership and sensorimotor coding in peripersonal space

## 3. RATIONALE OF THE THESIS

#### 3.1. THEORETICAL RATIONALE

In the previous sections, I showed that peripersonal space (PPS) is a dynamic and functionally grounded interface that supports interactions between the body and the environment. I demonstrated that stimuli occurring in this action-oriented space benefit from enhanced multisensory and sensorimotor processing. Such encoding supports both anticipatory response to threatening stimuli approaching the body, but also the initiation of purposeful actions toward objects within reach. This supports the view that PPS is composed of multiple graded fields that can be additive, each reflecting the behavioral relevance of a stimulus given a specific goal and context. The present thesis focuses specifically on the instrumental, motor-related function of PPS, in which spatial representation is constructed relative to action potential.

I then discussed how PPS supports not only physical interaction with items but also social interaction, thus adapting to social context: the presence and behaviour of others can expand or constrain the spatial encoding of reachable space and, during social interaction, PPS can become partially co-represented to reflect common goals. Specifically, among the various social and contextual cues that modulate spatial encoding, ownership plays a central role, as it imbues objects with specific value: it engages both self-referential and social processes, which contributes to the distinction of what is "mine" (i.e., relevant to me) and "yours" (i.e., relevant to others). Ownership therefore acts as a cognitive bridge between the embodied self and the social world by attributing personal significance to external items. Although ownership is highly relevant to physical interaction, it has often been studied in abstract or non-ecological settings through labels, symbolic associations, or with centrally presented objects on screen, neglecting its central action-related dimension.

#### 3.2. Research question

## 3.2. RESEARCH QUESTION

While a growing body of evidence supports the notion that object ownership enhances cognitive processing toward self-related stimuli, it is not clear whether these effects depend on the spatial location of objects. Previous studies have primarily used paradigms in which object ownership was dissociated from spatial positioning, often centrally presented. However, such a configuration neglects a critical feature of interaction: the body is situated in space, and action is constrained by spatial accessibility. If the influence of ownership derives from increased motivational value, as proposed in frameworks linking ownership to goal relevance (Constable et al., 2011; Truong & Todd, 2017), then, such effects should manifest preferentially when an object is within reach, where it is actionable.

Said differently, in real-world (spatialized) interactions, not all objects hold the same value or meaning. Unlike in a highly-controlled standardized experimental context, where participants interact with stimuli that are virtually identical, the objects we can or intend to interact with differ substantially in their significance and relevance. Thus, while it is well-established that certain physical properties of objects (e.g., luminance, color, threat-related features) can disrupt or modulate their encoding, there is still little insight into the influence of conceptual factors, despite their frequent occurrence in everyday life. These reflections lead to a central research question:

Is there an interplay between spatial location and ownership in the processing of objects?

Or, more specifically:

Does the influence of object ownership on behavioral and neural processing depend on the object's location in space, specifically, whether it is located inside or outside the actionable space?

#### 2.3.2. Ownership and sensorimotor coding in peripersonal space

This question brings two closely related theoretical considerations, each addressing the same underlying issue from a different perspective. First, does the self-prioritization observed for owned objects reflect a purely abstract and symbolic association, or is it embodied and grounded in an action-oriented context? Said differently, is the encoding of objects for interaction strictly determined by physical and spatial factors, or can it also be shaped by higher-order conceptual characteristics?

Both theoretical questions lead, at an empirical level, to the same testable prediction: that the prioritization driven by ownership will manifest more robustly for objects located within the space where direct interaction is possible, that is, in the PPS. This assumption raises important additional questions: does this self-prioritization enhance action-related processes, or does it reflect a general early attentional bias (as described in the SAN, Humphreys & Sui, 2016; Sui & Rotshtein, 2019)? Furthermore, is the boundary of PPS representation recalibrated depending on whether available objects are owned by oneself or another person? Finally, if spatial location and ownership interact in object processing, what are the neural mechanisms underlying this interaction?

#### 3.3. METHODOLOGICAL RATIONALE

Through several studies, we aimed at investigating how object ownership modulated PPS representation and the processing of objects in PPS. To this end, we employed the well-established paradigm of the reachability judgement task, whose choice was driven by considerations mentioned in section 1.2.4. In the first experiment, we conducted this task by implementing the constant-stimuli method by presenting self- and other-owned objects at a range of spatial locations distributed along the participant's sagittal axis. This allowed us to derive psychometric curves plotting the probability of a positive answer to the reachability judgement across distance and to estimate the inflexion point of the logistic curve, which serves as an operational measure of the

#### 3.3. Methodological rationale

PPS boundary. This approach enables a continuous assessment of PPS representation, in contrast to a binary near / far categorization. In the following studies, to enhance the contrastive power of the paradigm and isolate more clearly the interaction between spatial location and ownership, we adapted the constant-stimuli method by categorically dividing space into peripersonal and extrapersonal sectors based on individually calibrated thresholds derived from prior reachability judgements. This binary spatial division, while less fine-grained than the continuous method, facilitates direct statistical comparison of behavioral and neural responses between spatial zones, improves sensitivity, and reduces the required number of trials, especially in longer designs (such as in the fMRI study). In addition, we interleaved randomly trials in which self- or other-owned objects appear at each distance to prevent strategic adaptation or anticipatory biases and to ensure that each judgment reflects an online estimation of action possibility.

While designing these studies, a major methodological concern was to isolate the cognitive effects of ownership from those of other forms of self-relevance, particularly a history of utilization or manipulation, personal identity, affective attachment, or semantic associations. In naturalistic contexts, objects that we own are typically those with which we interact frequently, over which we exert control, and which may carry emotional or autobiographical significance. These factors, while enriching and strengthening the psychological bond between the owner and the object, confound the attribution of any observed behavioral or neural effect strictly to ownership *per se*. To overcome this issue, we designed the allocation of ownership in a way that the same physical objects were used across all experimental conditions and were assigned to either the participant ("self-owned") or to another individual, here, a virtual character ("other-owned"). Ownership was induced through explicit instructions rather than through extended use or personalization, thereby avoiding uncontrolled variance in the depth or type of self-object association, which aligns with

existing paradigms that demonstrate reliable self-prioritization effects following minimal ownership induction (e.g., Golubickis et al., 2018; Sui et al., 2012). This strategy ensured that all perceptual and functional properties of the stimuli were held constant, and that any modulation of behaviour or brain activity could be attributed to ownership rather than to the physical characteristics or a specific history of the object. Ownership was not mentioned in the instructions of the reachability judgement task to ensure that any observed modulation in the dependent variables reflects incidental processing of ownership cues, rather than task-induced prioritization (Golubickis & Macrae, 2023).

Another important methodological decision concerns the contrast structure used for evaluating ownership effects. Rather than using a "neutral" (non-owned) object as a control condition, we chose to contrast "self-owned" objects with "other-owned objects". This decision was motivated by several considerations: first, in ecological terms (especially in Western societies), it is rare to encounter manipulable, manufactured objects that are truly "non-owned". Even objects located in shared spaces (e.g., urban furniture, public goods) are typically understood to be owned collectively or managed by an institutional actor. Presenting an object as non-owned could introduce interpretive ambiguity: some participants may infer that the object is free for interaction or even belongs to them (Patané et al., 2021; Scorolli et al., 2018), while others may presume it to be implicitly owned by the experimenter or by a third party, which introduces an unknown variance in ownership-related processing. Second, prior research suggests that ownership is attenuated or disappears in the absence of a social counterpart (e.g., Constable et al., 2014). This raises conceptual questions: can objects be experienced as "mine" in a functionally relevant way if there is no "yours"? More broadly, can self-related processing be fully engaged in the absence of any distinction from others? These questions have been extensively debated in the literature on the self

#### 3.4. Overview of the studies

(e.g., Gallagher, 2000; James, 1890) and refer to the idea that self-relevance is inherently relational: meaningful distinctions emerge only in contrast to a referent other. To preserve interpretive clarity, we adopted a self vs. other framework, operationalizing "other" as a neutral stranger rather than a relative or friend. While other studies have used significant others as comparison targets, such designs may raise the concern about the infusion of self into the concept of "other" (Aron et al., 1991; Symons & Johnson, 1997). This methodological decision thus aligns with a theoretical standpoint: while ownership may modify how one processes objects, it does so in relation to a social context, which determines the normative implications of that ownership. In this context, the self/other contrast provides a clearer interpretive framework.

#### 3.4. Overview of the studies

Chapter 4 explored the first central question of this thesis by seeking behavioral evidence of the interplay between spatial location and ownership. Specifically, investigated whether the representation of the PPS was modulated by the ownership of objects, and whether the prioritization of owned objects depended on their spatial location. To answer these questions, we employed a reachability judgement task, in which participants were asked to estimate the reachability of a self- or an other-owned cup. This was combined with a localization task where participants had to indicate the previous location of the above-mentioned cups. This design enabled us to examine (i) if object ownership interacted with spatial location in the processing of objects for interaction, (ii) if object ownership directly modulated the representation of the PPS, and (iii) if ownership modulated the spatial reference frame adopted to encode these objects. This approach offered a behavioral characterization of how spatial and ownership information interact in object representation, and whether ownership influences not only action-related judgements but also the spatial representation of objects in a social context.

#### 2.3.2. Ownership and sensorimotor coding in peripersonal space

In Chapter 5, we extended this approach by examining whether object ownership modulates inhibition control. Indeed, we hypothesized that the prioritization of self-owned objects in the PPS mainly serves to enhance the efficiency of action, and thus posited that executive control, and more specifically inhibition, would reflect a similar prioritization. To test this hypothesis, we integrated electromyographic recordings into an adapted version of the paradigm used in Chapter 4 to assess the proportion and temporality of partial errors (i.e., small erroneous activations that were corrected online) as an index of inhibition control efficiency. This indicates whether the prioritization of owned objects in the PPS operates via improved online control over action plans.

In chapter 6, we further investigated the temporal dynamics underlying the interaction between spatial position and ownership. Although theoretical models of PPS and self-prioritization both posit early processing advantages, it remains unclear if these prioritizations exert their influence at distinct or overlapping temporal stages of object processing for goal-directed action. To address this, we used EEG to test if these two prioritizations (induced by ownership, and induced by a location in the PPS) each occur during early perceptual stages, or if they reflect later, context-dependent evaluative processes.

In chapter 7, we aimed to identify the neural substrates supporting the integration of spatial and ownership-related information during object processing. While the PPS has been associated with parietal and premotor regions involved in action preparation and execution, and object ownership has been linked to frontal areas implicated in both social and self-referential processing, how these neural systems influence each other when spatial and conceptual dimensions converge remains unknown. The fMRI study presented in this chapter was designed to clarify whether the neural representation of object ownership is spatially organized, and whether regions involved in the processing of objects in the PPS differently encode objects as a function of their ownership.

# 3.4. Overview of the studies

By combining univariate and multivariate analyses, we examined whether ownership modulates brain activity in ways that are contingent upon the object's location in actionable space.

# Part II EXPERIMENTAL CONTRIBUTION

#### 4.1. Foreword

# 4. OBJECT CODING IN PERIPERSONAL SPACE DEPENDS ON OBJECT OWNERSHIP

#### 4.1. Foreword

In the introduction, we established that PPS functions as a specialized interface for both object-directed and social interactions, and that its dimensions were modulated by various factors. However, despite major findings in understanding the influences of object-related and social variables on PPS plasticity, no study has yet addressed how these two types of information may interact. This question is particularly relevant as social information can be embodied not only by other individuals, but also by objects themselves, which carry ownership information most of the time in daily life.

We hypothesized that self-ownership facilitates the processing of objects in PPS, where actions are directly possible. Specifically, using a reachability judgement task, we expected faster RTs for self-owned compared to other-owned objects, but this facilitation would be restricted to objects located within PPS. Furthermore, we predicted that in contexts where the reachability judgement task is more difficult, such as at the boundary of PPS, ownership would serve as an additional cue supporting action decision, resulting in a decisional bias that extends the perceived boundary of PPS. In addition, considering that ownership may be encoded or may influence an object's processing differently as a function of individual social abilities, we examined whether differences in empathy correlated with the ownership-induced modulation of the PPS boundary.

Finally, in an exploratory manner, we also investigated whether the interaction between spatial location and ownership influenced the spatial reference frame (egocentric or allocentric) used to encore objects information.

#### 4.2. MAIN STUDY

# OBJECT CODING IN PERIPERSONAL SPACE DEPENDS ON OBJECT OWNERSHIP

Lucie Lenglart<sup>a</sup>, Alice Cartaud<sup>a</sup>, François Quesque<sup>b</sup>, Adriana Sampaio<sup>c</sup>, Yann Coello<sup>a</sup>

- a. Univ. Lille, CNRS, UMR 9193 SCALab Sciences Cognitives et Sciences Affectives, F-59000 Lille.
- b. Univ. Lille, Inserm, CHU Lille, U1172 LilNCog Lille Neuroscience & Cognition, F-59000 Lille.
- c. Psychological Neuroscience Lab, CIPsi, School of Psychology, University of Minho, Campus de Gualtar, 4710-057, Braga, Portugal.

Running title: Ownership and frame of reference in peripersonal space

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#### 4.2.1. Abstract

Previous studies have shown that objects located in the peripersonal space (PPS) receive enhanced attention, as compared to extrapersonal space (EPS), However, most objects in the environment belong to someone in particular and how object ownership influences object coding in relation to PPS representation is still unclear. In the present study, after having chosen their own mug, participants performed a reachability judgment task of self-owned and other-owned mugs presented at different distances while facing a virtual character. This task was followed, on each trial, by a localisation task in which participants had to indicate where the mug, removed from view, was previously located. The two tasks were separated by a 900 ms visual mask during which the virtual character was unnoticeably shifted by 3° to evaluate the spatial frame-of-reference used. The results showed that self-owned mugs were processed faster than other-owned mugs, but only when located in the PPS. Furthermore, reachability judgments were biased for self-owned mugs, leading to an extension of the PPS representation, especially for participants with a high score on the fantasy scale of IRI. Finally, the virtual character shift altered the localisation performance but only for the distant mugs, suggesting a progressive shift from egocentric to allocentric frame-ofreference when moving from the PPS to EPS, irrespective of object ownership. Overall, our data reveal that the representations of ownership and PPS interact to facilitate the processing of manipulable objects, to an extent that depends on individual sensitivity to the social presence of others.

#### 4.2.2. Introduction

#### 4.2.2. Introduction

The peripersonal space (PPS) is the space surrounding the body, in which interactions with the environment are achievable through body movements (Rizzolatti et al., 1981). The scientific consensus is that PPS represents a functional interface between the body and the environment that mediates perceptual attention toward objects that are relevant for voluntary motor action or that represent a source of hazard to the body (Belardinelli et al., 2018; Brozzoli et al., 2012; Coello & Cartaud, 2021). Accordingly, objects in the PPS benefit from enhanced perceptual and cognitive processing that motivates approach-avoidance behaviour depending on their appetitive or aversive value (Coello et al., 2018; Corr, 2013; Gigliotti et al., 2021). Enhanced processing of objects in the PPS was found in various paradigms including perceptual judgement (Iachini et al., 2017), perceptual categorization (Blini et al., 2018) and motor decision (Costantini et al., 2011; Wamain et al., 2016) tasks. Moreover, objects coding in the PPS entails multisensory integration in relation to the motor system (Bartolo et al., 2014b; Bassolino et al., 2015; Cardellicchio et al., 2011; Delevoye et al., 2010; Grade et al., 2015; Morgado et al., 2013; Wamain et al., 2016). Specifically, the presence of a stimulus in the PPS facilitates the processing of sensory input from the body (e.g., tactile) as well as sensory input from the stimulus (e.g., visual, auditory), as compared to the same stimulus presented outside the PPS, i.e. in the extrapersonal space (EPS hereafter). This facilitation effect is subtended by multisensory neurons characterized by overlapping receptive fields for object-related and body-related sensory signals, in a frame of reference anchored on a body segment (hand or head) or on the trunk (Serino et al., 2015; Zanini et al., 2021).

In agreement with a perceptually-induced activation of the sensorimotor network allowing the anticipation of possible actions (Anderson et al., 2002; Bourgeois & Coello, 2012; Iachini et

al., 2014; Phillips & Ward, 2002; Symes et al., 2005), objects in the PPS activate a fronto-parietal neural network that partially overlaps with the neural network underlying voluntary motor action and motor imagery (Bartolo et al., 2014b; Cléry et al., 2018). This network includes the premotor cortex (Caggiano et al., 2009; Graziano et al., 1994; Rizzolatti et al., 1981), the putamen (Graziano & Gross, 1993) and the parietal cortex (Colby et al., 1993), in particular its posterior part (area 7b, Graziano & Cooke, 2006) as well as the ventral and medial intraparietal areas (Colby et al., 1993; Colby & Duhamel, 1996). Congruent with an involvement of motor areas, EEG alpha-like μ rhythm desynchronization which is typically reported in situations associated with actual, imagined or observed motor actions (Babiloni et al., 1999; Braadbaart et al., 2013; Cochin et al., 1999; Hari, 2006; Llanos et al., 2013; Muthukumaraswamy et al., 2004; Pineda et al., 2000; Salenius et al., 1997; Salmelin & Hari, 1994), is also found during passive observation of manipulable objects (Proverbio, 2012), although only when presented in the PPS (Wamain et al., 2016).

Previous studies have suggested that the sensorimotor coding of objects in the PPS predominantly involves an egocentric spatial frame of reference (Alsmith, 2021; Bufacchi & Iannetti, 2018; Coello & Cartaud, 2021; Grade et al., 2015). As evidence, egocentric spatial coding is faster and more accurate than allocentric spatial coding (Millar, 1994; Ruggiero et al., 2016), and more sensitive to motor interference although exclusively in the PPS (Iachini et al., 2014). For instance, concurrent motor action (Grade et al., 2015), constrained arm posture (Ruggiero et al., 2021; Toussaint et al., 2020) and transient or permanent alteration of the sensorimotor system (Bartolo et al., 2014a), significantly impaired egocentric tasks such as memory-based spatial judgments or action-dependent judgments. These effects were however observed mostly for stimuli presented in the PPS. These findings led to the view that egocentric coding predominates

#### 4.2.2. Introduction

in the PPS (i.e. the space where there is direct interaction between objects and the body), whereas allocentric coding predominates in the EPS (i.e. where objects are out of arm's reach, Berti et al., 2001; Ruggiero et al., 2009; Weiss et al., 2003). A number of studies investigating the cerebral organisation of spatial processing in rodents, non-human primates and humans, and many behavioural studies have provided additional support for this functional specialisation of spatial coding (Bird & Burgess, 2008).

The fact that PPS related brain regions play a key role in the selection of visually guided actions and facilitate the interactions with manipulable objects (Bogdanova et al., 2021; Coello & Cartaud, 2021), implies that the representation of PPS must be flexible and adapt to the current state of both the body and the environment. Accordingly, changing the environmental constraints (Coello et al., 2018), objects properties (Gigliotti et al., 2021), or bodily disposition for action (Bourgeois et al., 2014; Quesque et al., 2017) was found to alter the representation of the PPS. As evidence, a shrinkage of PPS representation was reported following a reduction in the physical amplitude of manual actions resulting either from a stroke in the motor areas leading to hemiplegia (Bartolo et al., 2014a), amputation of a body limb (Makin et al., 2010), or transient immobilisation of the arm with a splint even for a few hours (Toussaint et al., 2020). By contrast, it has been shown that using a tool that provides a functional extension of the arm produces an extension of the PPS representation (Berti & Frassinetti, 2000; Biggio et al., 2017; Farnè et al., 2000; Maravita et al., 2000; Quesque et al., 2017; Serino et al., 2015; Witt et al., 2005). The same effects on the representation of the PPS were found when the objects in the PPS had a distinctly positive or negative valence (Coello et al., 2012; Gigliotti et al., 2021). Likewise, changing reward perspectives associated with motor actions toward objects in the PPS alters its representation (Coello et al., 2018; Gigliotti et al., 2021). Actually, biassing the distribution of reward-yielding

stimuli toward the distal or proximal region of the PPS produces respectively an increase or decrease in PPS representation (Coello et al., 2018), although the effect was attenuated in the presence of a partner implied in the task (Gigliotti et al., 2021). This clearly indicates that the representation of the PPS is not only underpinned by current motor abilities, but also by the expected advantages of acting toward one or another stimulus in the surroundings (Fujii et al., 2007), leading to the prioritisation of specific areas around the body at the expense of others (Coello et al., 2018; Fujii et al., 2008; Gigliotti et al., 2021). In social context, this prioritisation also integrates other agent's actions in relation to one's own actions (Fujii et al., 2008). Considered altogether, these data support the view that PPS representation stems from the integration of multiple factors including the agents' characteristics, the stimuli valence, but also the social dimension of the situation (Bogdanova et al., 2021; Coello & Cartaud, 2021; Gigliotti et al., 2021; Teneggi et al., 2013).

While originally conceived as an interface between the body and the environment, the PPS is thus increasingly considered as an interface between self and others (Cartaud et al., 2018; Coello & Cartaud, 2021; Teneggi et al., 2013). Within this growing interest in including the social dimension of PPS into a more comprehensive theoretical framework, it seems apparent that not only the physical but also the social characteristics of objects in the PPS are especially relevant. In particular, it seems likely that whether an object in the PPS targets the action of one person or another would modulate not only the coding of this object, but also the representation of the PPS. In accordance with this view, stimuli near the body are perceptually more salient when they are relevant for oneself but not for others (social association, Humphreys & Sui, 2015), leading to more accurate control of object-directed motor actions (Belk, 1988; Teramoto, 2018). Accordingly, objects that we own are processed faster than objects owned by others (Constable et al., 2019) and

#### 4.2.2. Introduction

benefit from a memory advantage (Cunningham et al., 2008; Symons & Johnson, 1997). This selfbias effect for initiation time to the self-owned objects was observed in both approach and avoidance tasks (Barton et al., 2021). Therefore, object ownership - which is conceived as a higherorder psychological construct that influences perceptual, cognitive and sensorimotor processes (Cunningham et al., 2008; James, 1890) - seems to be crucial in the selection of targets for motor actions (Constable et al., 2011, 2019; Desebrock et al., 2018). As evidence, in a task requiring participants to grasp and lift a mug, Constable et al. (2011) showed that participants put less force and acceleration in movements directed toward other-referenced objects, as if they cared more for the objects belonging to others. This effect was observed in adults and children as early as two years of age (Kritikos et al., 2020). Moreover, Constable et al. (2011) reported a spatial compatibility effect between the orientation of the handle of a mug and the location of the response key used to respond to a stimulus presented on the mug handle, although the effect was observed only when the mug was the participant's own mug. Overall, these data highlighted that object ownership is embodied within the sensorimotor system (Blakemore & Frith, 2003). They also suggest that the self can be extended beyond the body itself to encompass idiosyncratic experiences of objects (James, 1890), distinguishing thus items that are relevant for oneself from those that are not (Cunningham et al., 2008; Fujii et al., 2007). However, it is not clear yet whether the influence of object ownership depends on the location of the object in space. Indeed, if ownership property's influence can be explained by an increase in the motivational relevance of self-referenced objects as previously suggested (Constable et al., 2019), then benefits might only manifest where an action toward these objects is directly achievable, i.e., in the participant's PPS.

Within this context, the aim of the present study was to assess whether object processing was influenced by object ownership and location in space. We also assessed whether the spatial frame-of-reference used for object coding differs in PPS and EPS but depending on object ownership. Finally, we explored interindividual variability using a multifactorial measure of empathy abilities (IRI, Davis, 1983). To this end, we requested participants to first choose a mug as being their own among two possible choices. Then, they were requested to judge the reachability of self- vs other-owned mugs presented at different distances while facing a virtual character. This task was followed, on each trial, by a mug localisation task in which participants had to indicate where the mug, removed from view, was located before. The two tasks were separated by a 900 ms visual mask during which the virtual character was unnoticeably displaced laterally by 3°, in order to assess the spatial frame of reference predominantly used in the object coding as a function of distance and ownership. We predicted that objects in the PPS compared to the EPS would be processed faster, in particular self-owned objects compared to others-owned objects, using predominantly an egocentric frame of reference. We also predicted that reachability judgement should be biased toward self-owned objects, leading to an extension of PPS representation.

#### 4.2.3. *Method*

#### **Participants**

40 French voluntary participants completed the experiment (29 females and 11 males, mean age = 22.65, SD = 2.66). They were recruited through ads posted on online student forums. Participants were right-handed, had a normal or corrected-to-normal visual acuity and declared having no neurological, psychiatric or visual trouble likely to interfere with the course of the experiment. The experimental protocol was conducted in accordance with the ethical principles of

the Declaration of Helsinki (World Medical Association, 2013) and was approved by the University of Lille Institutional Ethics Committee (Ref. Number 2021-518-S95). Participants received an information letter and gave their informed consent prior to the experiment onset.

#### Materials and design

Object ownership was induced at the beginning of the experiment by making the participants choose a physical mug among two which differed by their colour (yellow or blue coloured dots on a dark mug). The participants could manipulate their mug for a few minutes before the experiment started and were informed that the mug they selected would be assigned to them for the whole experiment. The participant was informed that the other mug would be attributed to the virtual character involved in the different tasks performed in a virtual room. The mugs were virtually replicated as the experimental tasks were fully computerized.

The whole experiment was created on lab.js (Henninger et al., 2020). It was conducted on a 23" screen (1920 x 1080 pixels) located at a distance of 60 cm from the participants and connected to a computer (Dell Precision T1700). The experiment consisted of an Implicit Association Test (IAT, Greenwald et al., 1998), a reachability judgement task, an object's localisation task and ended with the completion of the Interpersonal Reactivity Index (IRI, Davis, 1983). Except for the IAT, the experiment was conducted using pictures generated on Unity composed of a 150 cm long table at the extremity of which a neutral-faced male virtual character taken from the ATHOS database (Cartaud & Coello, 2020) was seated (see Figure 8). The character was randomly located either to the left (-3°) or right (+3°) of the participant's body mid-sagittal axis (see Reachability and Object localisation tasks section). Participants were requested to represent themselves as if they were sitting at the proximal edge of the table in the virtual

environment. The stimuli consisted of two virtualized mugs with one attributed to the participant ('my mug', i.e. self-owned mug) and the other to the virtual character ('his mug', i.e. other-owned mug), depending on the participant's initial colour choice. The coloured dots on the mugs were isoluminant on Unity (HSV 100% luminance), and their isoluminance was quasi-identical as measured on the computer screen (on average 50 lx) with the Konica Minolta T-10A illuminance metre. In the reachability judgement task, each of the two mugs was randomly and individually presented at 15 distances (ranging from 5 cm to 145 cm from the proximal edge of the virtual table, with an inter-target distance of 10 cm) at either -3° or +3° from the participant's body mid-sagittal axis, in order to be aligned with the virtual character. In the object's localisation task, the virtual scene was the same except that the mug was removed and the virtual character was moved by  $\pm 3^\circ$ , and thus located at  $\pm 6^\circ$  from the participant's body mid-sagittal axis. To avoid visual remanence, a grayscale mask (1080 x 1920 pixels randomly positioned and ranging from black (0, 0, 0) to white (255, 255, 255) on the RGB colour space, average luminance 18 lx) was displayed for 900 ms after each trial on both the reachability judgement task and the object's localisation task (see Figure 8).

# Procedure

Participants first had to select a mug that would be their own mug during the whole experiment, among two possible coloured physical mugs. They were informed that the other coloured mug would be attributed to the virtual character. They were then invited to sit in front of the computer's screen and had to confirm their mug selection by ticking a radio button under the corresponding mug's picture. The instructions for each task were displayed on the screen before each task. The whole experiment lasted approximately 25 minutes.

#### **Implicit Association Task**

The IAT was adapted from a similar test designed by LeBarr and Shedden (2017). In this task, participants had to associate (1) words related to themselves or to the virtual character to individual-related categories and (2) pictures of the virtual mugs to mug-related colour categories. Specifically, the two categories were displayed on the left and right upper side of the screen and respectively associated with the 'E' or 'I' response key (French AZERTY keyboard). The individual-related categories were 'Name of the participant' for the participant and 'Avatar' for the virtual character. The associated words to categorise were respectively 'Moi' (Me), 'Je' (I), 'Soi' (Self), 'Lui' (Him), 'II' (He) and 'Autrui' (Other). The two mug-related colour categories were labelled 'Bleu' (Blue) and 'Jaune' (Yellow) and the associated pictures to categorise were pictures of the two virtual mugs (with a yellow or blue dot) with different orientations (handle oriented to the left, to the right, or not visible). The stimuli to be categorized (words or pictures) were displayed at the centre of the screen on a white background. As participants previously chose their own-coloured mug, the colour categories also incidentally corresponded to object ownership.

To perform the IAT, participants were asked to associate, as quickly and accurately as possible, stimuli (words and pictures) with category labels presented at the right or the left upper side of the screen. The categories' sides were counterbalanced between participants. For each trial, a stimulus (a word or a picture) was randomly presented at the centre of the screen until the participant categorized it. If the response was correct, a 900ms blank screen was displayed before the beginning of the next trial. If the response was incorrect, a red X appeared under the stimulus and participants had to correct their response in order to continue. The task was composed of 7 blocks (see Table 1 for a description of the blocks). In the first four blocks, one keyboard key (e.g., 'E') was associated with the colour of the participant's mug and the name of the participant; the

other key (*e.g.*, 'I') was associated with the colour of the virtual character's mug and the word 'Avatar' (congruent blocks). In the first block (24 randomized trials), participants only categorized the six mug pictures (each presented four times) into the colour categories (yellow-blue). In the second block (24 randomized trials), participants only categorized the six words (each presented four times) into the self-related categories ('Name of the participant' - 'Avatar'). In the third (24 randomised practice trials) and fourth block (48 randomised test trials), participants categorised both words and pictures (each presented 6 times, congruent blocks). The last three blocks were identical to the three previous ones, but the response code was reversed for the colour categorisation only (incongruent blocks). More precisely, the name of the participant was associated with the same key as previously (*e.g.*, 'E'), but the colour of the participant's mug was associated with the other key (*e.g.*, 'I', see Table 1). By comparing the response times in congruent and incongruent blocks, the IAT provides a measure of the strength of associations between categories (Greenwald & Nosek, 2001).

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Block	Function	Trials number	Categories
1	Practice	24	Mug colour
2	Practice	24	Self-related words
3	Congruent Practice	24	Mug colour + Self-related words
4	Congruent Test	48	Mug colour + Self-related words
5	Practice	48	Mug colour
6	Incongruent Practice	24	Mug colour + Self-related words
7	Incongruent Test	48	Mug colour + Self-related words

Table 1. Description of the Implicit Association Task.

# Reachability judgement task

In the reachability judgement task, participants estimated whether the mug displayed was reachable with their right hand or not depending on its location in the virtual environment, without performing any movement. The mug displayed could be the mug belonging to the participant (own-mug) or to the virtual character (other-mug). Responses were provided by pressing on the 'C' keyboard key with their left index finger if the mug was reachable or the 'X' keyboard key with their left middle finger if the mug was judged unreachable (response keys were counterbalanced across participants). The two mugs were each presented two times at each of the 15 distances and for the two virtual characters' locations (± 3°), for a total of 120 trials (2 mugs x 15 distances x 2

avatars' locations x 2 repetitions). On each trial, after the participant's response, the random-dots mask was displayed for 900 ms before the onset of the object localisation task.

## Object localisation task

The object localisation task was embedded in the reachability judgement task, and participants successively responded to both tasks for each trial (see Figure 8). In this task, the virtual scene was the same as the one just presented for the reachability judgement but without the mug. Moreover, the virtual character was moved to  $\pm 6^{\circ}$ , thus  $\pm 3^{\circ}$  according to its previous location. On every trial, the task was to point the location of the coloured dot of the mug which was presented during the reachability judgement task with the mouse cursor. A random-dots mask was displayed for 900 ms after the participant's response, thus before triggering the next trial of the reachability judgement task. The mouse cursor was only visible during the localisation task, which prevented gathering any spatial information during the reachability judgement task.

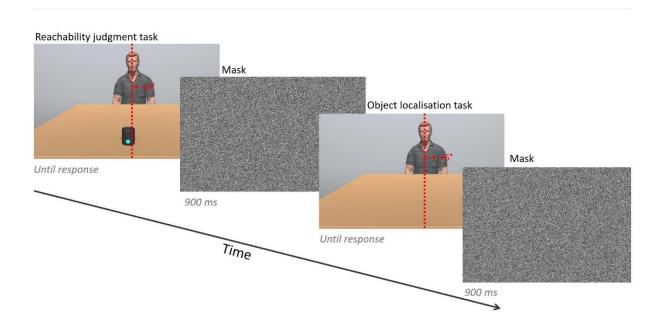


Figure 8. Illustration of the experimental set-up and time course for one trial including the reachability judgement task and the object localisation task. Note that the 900-ms random-dot mask was displayed before the beginning of each task. The mug just presented in the reachability judgement task was removed from view in the object localisation task. The red dashed line represents the centre of the table. Note that the virtual character, initially set at  $\pm 3^{\circ}$  in the reachability judgement task was unnoticeably shifted at  $\pm 6^{\circ}$  according to the centre of the virtual table in the object localisation task.

#### Interpersonal Reactivity Index

At the end of the experiment, participants were asked to complete the French version of the IRI (Davis, 1983; Gilet et al., 2013) to assess empathy skills. The questionnaire, presented on the computer screen, was composed of 28 items divided into four subscales: Personal Distress (PD), Empathic Concern (EC), Fantasy Scale (FS) and Perspective Taking (PT). Responses were provided using a 5-point Likert-type scale ranging from 1 ('does not describe me well') to 5 ('describes me very well'). The scale was presented under each item and all the items were presented on the same page. There was no time constraint and the participants could change their responses until they validated the whole questionnaire.

# Data analysis

The data processing and analyses were conducted on R version 4.1.1 (R Core Team, 2020). Before all parametric analyses, the normality assumption was controlled using the Shapiro-Wilk test and the sphericity assumption was verified using Mauchly's sphericity test. Analysis of variance (ANOVA) was computed with the 'rstatix' package (Kassambara, 2021). When normality of the distribution was not verified, non-parametric permutation-based ANOVA (Kherad-Pajouh & Renaud, 2015) was conducted using the 'permuco' package (Frossard & Renaud, 2021), and following post-hoc comparisons were performed using the 'MKinfer' package (Kohl, 2020). Significance threshold was set at  $\alpha = 0.10$  for tests verifying the assumptions required for the application of parametric tests and at  $\alpha = 0.05$  for statistical tests. Post-hoc comparisons were performed using Bonferroni's correction and effect sizes were determined with partial Eta-squared ( $\eta^2$ p).

# **Implicit Association Task**

Following an improved IAT scoring algorithm (Greenwald et al., 2003), trials with an RT superior to 10 s were discarded, and only the data from Congruent (3 and 4) and Incongruent (7 and 8) blocks were analysed (see Table 1). Mean RT of correct trials in the Congruent and Incongruent blocks were calculated separately, and a pooled standard deviation was computed for Practice (3 and 7) and Test (4 and 8) blocks. RT of trials that resulted in an erroneous response were replaced by the mean of the corresponding block type (Congruent/Incongruent) to which were added 600 ms (4.8 % of the data, see Greenwald et al., 2003). The difference between the Incongruent and Congruent blocks was computed for both the Practice and the Test blocks and

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was divided by their associated standard deviations. Finally, the two quotients obtained were computed to obtain a single D score that can be interpreted as the Cohen's d: the d < 0.2 reveals no association, a slight association between 0.2 and 0.5, a medium association between 0.5 and 0.8 and a strong association beyond 0.8. The mean D was calculated across participants to estimate the mean size of the association strength between the participants' mug colour and the words related to themselves.

# Reachability judgement task

Based on reachability (yes-no) responses, the threshold corresponding to the maximum reachable distance was calculated using the following equation:

$$y = exp(\alpha + \beta x) / (1 + exp(\alpha + \beta x))$$

Where x represents the distance of the mug, and y represents the participant's probability of answering 'reachable'. The goodness of fit of the model was calculated for each participant thanks to R-squared. The reachability thresholds (boundaries of the PPS) were determined by the value of x at which the transition from the response 'reachable' to 'unreachable' was made (inflexion point of the curve), corresponding to  $(-\alpha/\beta)$ . For each participant, we computed one reachability threshold per mug's ownership status (self-owned, other-owned). We then compared them through a within-subject Student's t-test. A higher reachability threshold in one condition expressed an extension of PPS representation, and conversely a lower reachability threshold expressed a shrinkage of PPS representation.

In addition, response time (RT) was registered. To analyse RT depending on the mugs' location, we divided the workspace into three equal areas computed according to the average

reachability threshold. The four nearest distances (5 cm, 15 cm, 25 cm and 35 cm) were classified as 'PPS', the four next distances (45 cm, 55 cm, 65 cm and 75 cm) were classified as 'boundary of PPS', and the four next distances (85 cm, 95 cm, 105 cm, and 115 cm) were classified as 'EPS'. Participants with more than 10 % of RT above 5000 ms were removed from the analysis (2 participants, 5.4 % of the dataset). For each participant and each area, RT inferior to 200 ms or superior to 2 standard deviations from their mean RT were discarded (5.3% of the dataset). Due to the lack of normality of the data distribution, RTs were analysed using an Ownership (self-owned, other-owned) × Space (PPS, boundary, EPS) permutation-based within-subject ANOVA (Kherad-Pajouh & Renaud, 2015). The number of permutations was set at 9999. Post-hoc comparisons were performed using pairwise t tests with 9999 Monte Carlo resampling and the p-values were corrected using the Holm-Bonferroni method (Holm, 1979).

# Object localisation task

The localisations of the mugs were registered from the 2D pixel coordinates of the computer mouse cursor (*i.e.*, the pointing positions of the mouse's cursor when clicking). For each distance, pointing positions deviating by more than two standard deviations from the mean position were considered as outliers and discarded (4.5% of the dataset). Data for all distances were analysed, with the exception of the 5 cm shorter distance due to performance over-variability when expressing the performance in angle. Because the mugs were presented at  $\pm 3^{\circ}$  from the mid-body sagittal axis in the reachability judgement task, pointing positions in the object localisation task were first realigned with a  $0^{\circ}$  referential axis. Data were thus normalised, assuming that the actual location of the mug at  $3^{\circ}$  corresponded to 0 and the theoretical location of the mug at  $6^{\circ}$  corresponded to 1 on the x-axis, whatever the distance. To do so, the exact position of the mug at

#### 4.2.3. Method

 $3^{\circ}$  was subtracted to each pointing position, and this difference was divided by the size of the computed vector (in pixels) between the  $3^{\circ}$  and  $6^{\circ}$  positions. The normalised positions obtained reflected a measure of the pointing error. A pointing error of 0 indicated an absence of deviation from the location of the mug previously displayed and therefore revealed the use of an egocentric (self-centred) framework for the spatial coding of the mug. Conversely, a pointing error of 1 indicated that the participant coded the spatial location of the mug in relation to the virtual character's location and therefore revealed the use of an allocentric (other-centred) framework. Data were then analysed using a 2 ×14 repeated measures ANOVA (2 Ownership status: me, him x 14 Distances) with Greenhouse & Geisser Epsilon Correction (Greenhouse & Geisser, 1959). Post-hoc comparisons were performed using pairwise repeated t tests and the p-values were corrected using the Holm-Bonferroni method (Holm, 1979).

# <u>Interpersonal Reactivity Index</u>

The results of the IRI were analysed by computing, for each participant, the score obtained in the different subscales (Personal Distress, Empathic Concern, Perspective Taking, Fantasy). To estimate the extent to which the different components of empathy were related to the changes in the reachability threshold depending on mug ownership, a multiple linear regression analysis was performed between the difference in reachability threshold (self-owned, other-owned) and the scores at the different subscales of IRI.

#### 4.2.4. Results

Post-experiment interviews revealed that none of the 40 participants identified the aim of the experiment. Also, no participants detected the shift of the virtual character in the localisation task. The data of three participants were removed from the whole data analysis because their scores in the reachability task exceeded the mean by more than two standard deviations (7.5% of the data).

#### *Implicit association task*

Participants' IAT score D (M = 0.41, SD = 0.45) revealed that participants developed, on average, a slight but near medium association between their own mug colour and themselves, suggesting the presence of a sense of ownership for the mug they initially chose.

### Reachability judgement task

The goodness of fit for logistic regression was individually checked, and the R-squared was on average 0.78 (SD = 0.15), suggesting a good fit of the sample data using logistic regression. Ownership (self-owned, other-owned) within subject Student's t-test was significant: the boundary of the PPS was estimated further away in the presence of self-owned (M = 56.74, SD = 10.52) compared to other-owned mugs (M = 54.61, SD = 10.84,  $t_{(36)} = 2.52$ , p = 0.008, d = 0.414, see Figure 9).

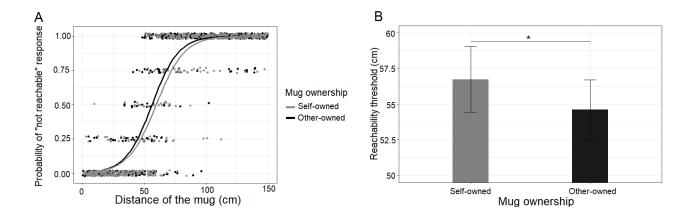


Figure 9. (a) Average probability of "not reachable" response for each participant as a function of distance and object ownership. The logistic function expresses the transition from reachable to unreachable mugs as a function of distance. The change in slope expresses the limit of reachability used as a proxy of the PPS boundary. (b) Mean reachability thresholds as a function of ownership (self-owned, other-owned). Error bars represent standard errors, and stars indicate significant differences in the reachability threshold change (\*p < .05)

The analysis of response time (RT) showed a main effect of Space ( $F_{(2,68)} = 44.90$ , p <0.001,  $\eta^2p = 0.56$ , see Figure 10). The observed effect was due to faster responses when the mug was located in the PPS (M = 1119.98 ms, SD = 303.40,  $t_{(69)} = 9.63$ , p < 0.001) and in EPS (M = 1169.68 ms, SD = 351.34,  $t_{(69)} = 9.69$ , p < 0.001) than at the boundary of PPS (M = 1496.05 ms, SD = 473.05). No significant difference was observed between PPS and EPS ( $t_{(69)} = 1.60$ , p = 0.057). A main effect of Ownership was also found ( $F_{(1,34)} = 4.20$ , p = 0.049,  $\eta^2p = 0.10$ ). Specifically, participants were faster to respond in the presence of self-owned (M = 1239.08 ms, SD = 404.91) compared to other-owned mugs (M = 1284.97 ms, SD = 427.46,  $t_{(104)} = -2.23$ , p = 0.014). Furthermore, results revealed a significant Space × Ownership interaction ( $F_{(2,68)} = 4.85$ , p = 0.009,  $\eta^2p = 0.16$ ). Post-hoc comparisons revealed that RT was shorter in the presence of self-owned compared to other-owned mugs, but only when the mugs were located in the PPS (self-owned: M = 1086.48 ms, SD = 303.19; other-owned: M = 1153.48 ms, SD = 304.27,  $t_{(34)} = 1.68$ , p = 0.021) or at the boundary of the PPS (self-owned: M = 1444.43 ms, SD = 464.35; other-owned:

M = 1548.39 ms, SD = 482.65,  $t_{(34)} = 2.58$ , p = 0.021). In the EPS, no difference was found in RT between self-owned and other-owned mugs (self-owned: M = 1186.32 ms, SD = 351.72; other-owned: M = 1153.045 ms, SD = 355.29,  $t_{(34)} = -0.977$ , p = 0.168).

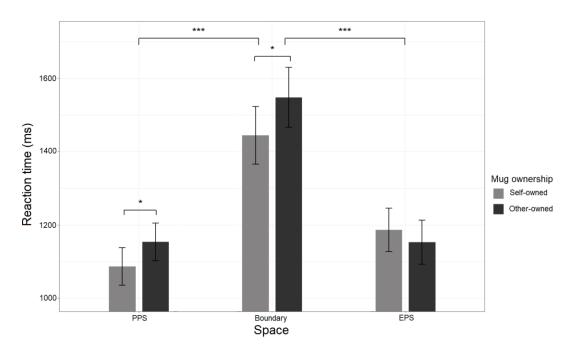


Figure 10. Mean RT as a function of space (PPS, boundary, EPS) and object ownership (self-owned, other-owned). Error bars represent standard errors and stars indicate significant differences (\*p < .05, \*\*\*p < .001).

#### Interpersonal Reactivity Index

Participants' IRI score was on average 90.13 (SD = 7.97). The regression model ( $R^2 = 0.22$ ) showed a positive association between the differences in reachability threshold (self-owned other-owned) and the score at the Fantasy subscale (M = 26.62, SD = 6.69,  $t_{(34)} = 2.85$ , p = 0.008), but not with the Empathic Concern score (M = 26.11, SD = 3.68,  $t_{(34)} = -0.86$ , p = 0.394), the Personal Distress score (M = 19.49, SD = 6.03,  $t_{(34)} = -1.14$ , p = 0.262), or the Perspective Taking

score (M = 26.19, SD = 3.87,  $t_{(34)} = 0.33$ , p = 0.740). Thus, the higher the score at the Fantasy subscale, the larger the difference between the reachability threshold for self-owned and other-owned mugs.

#### Localisation task

The pointing error was on average 0.32 (SD = 0.62). Results showed a significant effect of distance on pointing error ( $F_{(2,68)} = 44.90$ , p < 0.001,  $\eta^2 p = 0.56$ ). Pairwise comparisons showed that pointing error did not differ significantly from 15 cm to 115 cm (on average 0.29, SD = 0.34, all p > 0.05), but increased significantly at distances 125 cm to 145 cm (on average 0.48, SD = 0.28) when compared to all shorter distances (all p < 0.04, excepted for 15 cm due to over angular variability at the nearest distance, see supplementary material).

To summarise, the data analysis revealed that reachability judgments for self-owned mug were faster than for other-owned mug, although only when located in the PPS or at its boundary. Furthermore, a response bias was observed for a self-owned mug, leading to an increase in reachable responses for a self-owned mug. Finally, pointing error in the localisation task increased for mugs situated outside of the PPS, revealing a prevalence of self-centred frame-of-reference for the stimuli in the PPS and a shift toward an other-centred frame-of-reference for the stimuli outside the PPS, especially when considering the farthest unreachable distances. The fact that only a social stimulus was used, however, prevented us from discriminating the use of an other-centred frame of reference (*i.e.*, adopting the virtual character's perspective) from the use of an allo-centred (*i.e.*, using a disembodied perspective) frame of reference. In order to overcome this issue, we ran a complementary experiment. This supplementary experiment also gave us the opportunity to implement a "no shift" condition as the constant use of the 3° lateral shift of the virtual character

might have resulted in an underestimation of the influence of the context (in the absence of a baseline condition).

# 4.2.5. Complementary experiment

The complementary experiment was run using the same experimental setup and the same protocol as before, *i.e.*, a reachability judgement task followed by a localisation task, but using complementary conditions. The two tasks were repeated through four counterbalanced experimental conditions: the stimulus at the extremity of the table could be either a virtual character or a neutral object (lamp) of equal dimensions, and these stimuli could be either shifted before the localisation task by  $\pm 3^{\circ}$  or not (0°), leading respectively to a location at  $\pm 6^{\circ}$  or  $\pm 3^{\circ}$  according to the participant body mid-sagittal axis. Finally, as no effect of ownership was found in the previous localisation task, a neutral mug with a white dot was presented on the virtual table.

Twenty-four new participants (19 women, mean age = 22.67; SD = 2.63) took part in the experiment. They received an information letter prior to the experiment and gave their informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013). All participants were right-handed, had a normal or corrected-to-normal vision, and declared having no neurological or psychiatric trouble.

The pointing error was analysed using the same method as in the main experiment. A 2 × 2 × 14 repeated measures ANOVA with Greenhouse & Geisser Epsilon Correction (Scene change  $(0^{\circ}, 3^{\circ})$  x Stimulus (virtual character, lamp) x Distance (15 cm to 145 cm) showed a main effect of Scene change  $(F_{(1,23)} = 59.30; p < 0.001; \eta^2 p = 0.72)$ . Specifically, the  $0^{\circ}$  shift (M = 0.12; SD = 0.18) generated significantly less pointing error than the  $3^{\circ}$  shift  $(M = 0.33; SD = 0.29; p < 0.001, <math>t_{(23)} = 6.05$ ). Moreover, a significant interaction was found between Scene change and Distance

#### 4.2.5. Complementary experiment

 $(F_{(2.65, 60.88)} = 5.93 \; ; p = 0.002; \eta^2 p = 0.21)$ : post-hoc analysis revealed that the pointing error induced by the 3° change condition (75 cm: M = 0.31; SD = 0.17) significantly differed from the one induced by the 0° change condition from 75 cm onwards (75 cm: M = 0.11; SD = 0.07;  $t_{(23)} = 5.32$ ; p < 0.001; see Figure 11). No main effect of Stimulus ( $F_{(1, 23)} = 0.001$ ; p = 0.982) nor of Distance ( $F_{(3.46, 79.57)} = 2.59$ ; p = 0.051) was found. No significant interaction was found between Stimulus and Distance ( $F_{(2.93, 67.40)} = 1.28$ ; p = 0.289) nor between Stimulus and Scene change ( $F_{(1, 23)} = 2.15$ ; p = 0.156), and no third-level interaction was found between Stimulus, Scene changes and Distance ( $F_{(2.49, 57.29)} = 1.21$ ; p = 0.311).

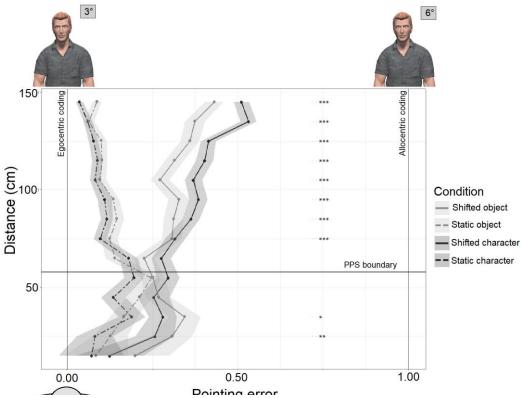


Figure 11. Mean pointing error as a function of distance and object ownership. Shaded areas represent standard errors and stars indicate significant differences between the pointing error when stimuli remained static (3°) and when stimuli were laterally shifted (6°) (\*p < .05, \*\*p < .01, \*\*\*p < .001). The dashed curves represent the performance in the virtual character (or object) no-shifted condition, whereas the plain curves represent the performance in the virtual character (or object) shifted condition. The grey curves the performance with the object, whereas the dark curves represent the performance with the virtual character.

The results of the complementary experiment showed that, at distances shorter than 75 cm, the pointing error in the 3° scene shifts condition did not differ significantly from the pointing error in the non-shift (control) condition and remained close to 0, suggesting a predominant use of egocentric spatial frame-of-reference for the shortest distances. However, the pointing error increased to approximately 0.5 when the scene was shifted compared to the control condition from the distance of 75 cm onward, suggesting a shift from egocentric to allocentric coding as the distance of the mug increased. The increase in pointing error with distance was irrespective of the type of stimulus present at the extremity of the virtual table, suggesting that the use of allocentric cues for distant objects was not determined by the social characteristic of the stimulus.

#### 4.2.6. Discussion

The present study aimed at assessing whether (1) ownership influenced object's processing depending on space, (2) ownership interacted with the representation of PPS and finally (3) ownership influenced the spatial frame-of-reference subtending object's coding in PPS and EPS. We will address these different issues after having discussed the validity of our paradigm.

Using a reachability judgement task as a proxy of PPS representation, we found that participants perceived the mugs at hand up to a distance of 56 cm according to the proximal edge of the virtual table, which corresponded to 37% of the table length. As previously described (Bartolo et al., 2014b; Coello et al., 2008; Leclere et al., 2020), we found an increase in response time for mugs located close to the boundary of the PPS (25% on average), compared to response time for mugs clearly located in the PPS or EPS (1028 ms on average). This increase of response time is compatible with the range of response time already reported (Bartolo et al., 2014b; Leclere et al., 2020), and can be accounted for by the fact that response time is generally higher when

uncertainty increases (Ratcliff & McKoon, 2008), which obviously rises as one approach the boundary of the PPS (*i.e.*, when both 'reachable' and 'unreachable' responses appear to be equally valid). The fact that the extent of the PPS representation was shorter than usually observed (*i.e.*, slightly wider than arm length when fully stretched, e.g. Leclere et al., 2020) can be accounted for by the fact that the virtual scene was in 2D and the computer screen was located at a fixed distance from the participant, possibly affecting the part of the virtual table that was perceived as reachable. An alternative interpretation could be that the task was performed in a social context. Indeed, Gigliotti et al. (2019) showed that when the workspace is shared between two confederates facing each other, object-directed motor actions for both confederates were located predominantly in the proximal space of the workspace associated with shrinkage of the PPS representation, compared to when performing the task in a non-social context (Coello et al., 2018). Further experiments would be needed to disentangle these different possible explanations.

A key outcome of the present study is that ownership influenced object's processing. The results indeed showed that response time was faster for self-owned mugs as opposed to otherowned mugs. This facilitation effect was earlier described as the self-prioritisation effect (Constable et al., 2019; Humphreys & Sui, 2015; Sui et al., 2012), and could be related to biased attentional saliency which influences perceptual processes in the presence of self-owned objects (Constable et al., 2019; Humphreys & Sui, 2015; Sui et al., 2012). This attentional prioritisation of self-owned objects may be driven by behavioral relevance (Constable et al., 2019): in contexts where ownership is relevant, self-owned objects would be attentionally salient in relation to one's own personal history of interactions with the environment (Todd et al., 2012), and the authority to act on self-owned objects (Truong & Todd, 2017). Here, the important finding is that the facilitation effect induced by self-owned objects was observed only for stimuli presented in the

participants' PPS or at the boundary of the participants' PPS. Since behavioral relevance is particularly significant in the participant's PPS because direct interaction with objects is expected, a possible interpretation could be that the sensorimotor coding of objects in the PPS is enhanced for self-owned objects in comparison to other-owned objects (Blakemore & Frith, 2003). Alternatively, and as suggested by Constable et al. (2011), the action system could be blind to the action potentialities associated with other people's objects, which could reflect social norms that prohibit interaction with objects belonging to others. In line with these assumptions, the difference in response time between self-owned objects and other-owned objects is particularly pronounced at the boundary of the PPS, a location where the role of the sensorimotor system has been reported to be determinant (Bartolo et al., 2014b; Caggiano et al., 2009; Coello et al., 2008; Hirose et al., 2010). Accordingly, and in accordance with Strachan et al. (2020), specifying whose space belongs to for action may serve to define the space in which object ownership leads to facilitated processing. Overall, the present study establishes that self-owned objects provide important social information contributing to facilitate stimuli selection in the PPS.

Another important result of the present study is that object ownership also influenced the representation of the PPS. Specifically, participants estimated their own mug as being more reachable than others' mugs, leading to an increase of 2.13 cm on average of the represented PPS in the presence of their own mug. This increase in PPS representation might be related to a decision bias induced by object ownership, in particular for objects located close to the boundary of the PPS (Coello & Bonnotte, 2013). Indeed, a decision bias is consistent with the sensorimotor coding of objects in the PPS as suggested above: assuming that the action system may be blind to the actions afforded by other-owned objects, participants may have better grasped the action potentialities of their own objects, thus their reachability, leading to an increase of PPS

representation in the presence of self-owned objects (or a shrinkage of PPS representation in the presence of other-owned objects). Similar decision bias has been reported in the past, as when, for instance, using spatial language in association with reachability judgments. Coello and Bonnotte (2013) indeed showed that the presentation of deictics referring to proximal, as compared to distal spaces, biased in the same way reachability judgements, resulting in an extension of PPS representation. Another possible interpretation could be that object ownership alters object valence, leading to a more positive valence attributed to self-owned as compared to other-owned objects, thus giving rise to an extension of the PPS representation (the mere ownership effect, Beggan, 1992). Congruently, previous studies revealed that changing the valence of objects in the PPS (Gigliotti et al., 2021) or outside the PPS (Bertonatti et al., 2021; Coello et al., 2012; Valdés-Conroy et al., 2012) induces a congruent change in the representation of the PPS. Overall, the presence of objects endowed with a positive valence would produce an extension of PPS representation, whereas the presence of objects endowed with a negative valence would produce a reduction of the PPS representation. Interestingly, we observed that the effect of self-owned objects on PPS representation was dependent on the score obtained by the participant at the Fantasy subscale of IRI. Specifically, the higher the score obtained by participants at the Fantasy subscale, the higher the extension of the PPS for self-owned mugs. The Fantasy subscale refers to people's propensity to get involved in fictional situations and to identify with fictional characters in virtual or imagined contexts (Gilet et al., 2013). Accordingly, the present results highlighted that the effect of object ownership might be dependent on the participants' capacity to consider the social presence of others, in particular when the situation implies virtual characters, such as in the present study. One may thus expect the effect of object ownership to be enhanced in ecological situations, which would be the focus of future experimental studies.

## 4.2. Main Study

The final key outcome of the present study concerns the spatial frame of reference used for object coding. We predicted that object coding would predominantly refer to an egocentric frameof-reference in the PPS and an allocentric frame-of-reference in the EPS, especially for self-owned objects as opposed to other-owned objects. Based on the results of the main and complementary experiments, our predictions were partially confirmed as the results revealed a predominant egocentric coding of the mugs when presented in the PPS and a significant change toward allocentric coding of the mugs when presented in the EPS. Indeed, the pointing error in the object localization task was significantly more influenced by the position of the virtual character (or the virtual object in the complementary experiment) facing the participants in the virtual room for distances from 75 cm onwards (therefore out of reach), while the pointing error was less determined by the position of the virtual character (or the virtual object) facing the participants for distances inferior to 75 cm. This revealed a lesser sensitivity to the context and thus a prevalence of egocentric coding for proximal mug locations. Therefore, the contribution of allocentric frameof-reference was found to grow when increasing the distance at which the mug was presented, suggesting a progressive shift in the frame-of-reference used in object coding when moving from clearly reachable to clearly unreachable objects. However, no effect of object ownership was found on the selected spatial frame-of-reference, even though object ownership was found to modulate the contribution of the motor system in object coding in the PPS. A potential explanation for the lack of effect of object ownership could be that objects processing is intrinsically dependent on an egocentric reference in the near space and an allocentric reference in the far space, as suggested by previous studies (Fini et al., 2015; Iachini & Ruggiero, 2006; Ruggiero et al., 2009). Another potential explanation could be that object ownership was irrelevant to complete the object localisation task (Constable et al., 2019), as the latter simply involved a comparison of perceptual

and memorised spatial information in a short time interval. Follow-up studies would be necessary to assess the effect of object ownership on memorised location of objects in situations in which there is an ecological advantage in remembering objects that belong to you, as opposed to those that belong to others (Cunningham et al., 2008; Iachini & Ruggiero, 2006).

Although the present study offers new insight into the influence of ownership in object coding depending on space, potential limitations of the study should be considered. First, the study was conducted with pictures projected on a computer screen, which might have amplified interindividual variability in spatial perception. In addition, the screen size was relatively small, which suggests that participants might have perceived distances to be further away than the actual metrics. An improvement that could be considered in the future would be to display pictures on a larger screen allowing the presentation of real spatial metrics, or to conduct similar study in a more ecological context using for instance immersive virtual reality. Another limitation was that ownership was limited to the selection of a mug just before the experiment onset. Confirming the present results while deepening the feeling of object ownership in different experimental situations would be an interesting challenge for the future. Finally, as already mentioned by Constable et al. (2011), it is not clear in the present study whether the effect of object ownership induced a facilitation of self-owned object processing or an inhibition of other-owned object processing. Analysing EEG signals and event-related motor potentials in addition to behavioural responses would represent new research avenues for deepening our understanding of the interaction between object ownership and spatial processing.

In conclusion, the present study revealed that object-related social information contributes to the perceptual processing of stimuli in the PPS, suggesting an embodiment of ownership in the sensorimotor system. Consequently, representations of object ownership and body-centred PPS

## 4.2. Main Study

interact so that the processing of action-related objects is facilitated, but to an extent that depends on individual sensitivity to the social presence of others. The outcome of the present study thus offers a new framework to investigate the behavioural aspects as well as the neural underpinning of object processing depending on both socially relevant and spatially relevant information. Beyond allowing a better grasp of the interplay between social cognition, object ownership and spatial representation, the original experimental paradigm developed in the present study could represent a valuable tool to investigate socially-relevant sensorimotor processing in clinical populations, in particular in populations characterised by social cognitive deficits.

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## **Declaration of conflicting interest**

The authors declare that there is no conflict of interest.

# 4.2.7. Supplementary information.

4.2.7. Supplementary information.

Pairwise comparisons using repeated t-test between error scores obtained in the no-shift condition (3°) and in the shift condition (6°) as a function of the distance (15 cm to 145 cm). Holm-Bonferroni corrected p-values are indicated. Text in bold indicates p < 0.05.

	15	25	35	45	55	65	75	85	95	105	115	125	135
25	1.00	-	-	-	-	-	-	-	-	-	-	-	-
35	1.00	1.00	-	-	-	-	-	-	-	-	-	-	-
45	1.00	1.00	1.00	-	-	-	-	-	-	-	-	-	-
55	1.00	1.00	1.00	1.00	-	-	-	-	-	-	-	-	-
65	1.00	1.00	1.00	1.00	1.00	-	-	-	-	-	-	-	-
75	1.00	1.00	1.00	1.00	1.00	1.00	-	-	-	-	-	-	-
85	1.00	0.63	1.00	1.00	1.00	1.00	1.00	-	-	-	-	-	-
95	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	-	-	-	-	-
105	1.00	0.12	0.11	0.88	1.00	1.00	1.00	1.00	0.22	-	-	-	-
115	1.00	0.07	0.07	0.39	1.00	1.00	1.00	1.00	0.06	1.00	-	-	-
125	0.46	<0.01	<0.01	<0.01	0.12	0.06	<0.01	<0.01	<0.01	0.04	0.38	-	-
135	0.12	<0.01	<0.01	<0.01	0.01	0.02	<0.01	<0.01	<0.01	<0.01	<0.01	1.00	-
145	0.12	<0.01	<0.01	<0.01	0.01	0.02	<0.01	<0.01	<0.01	<0.01	0.01	1.00	1.00

#### 5.1. Foreword

## 5. THE ROLE OF OBJECT OWNERSHIP ON ONLINE INHIBITION IN PERIPERSONAL SPACE

#### 5.1. Foreword

In the previous study, we found that reachability judgements were facilitated for self-owned compared to other-owned objects, but only in the PPS, where actions are directly executable. Following this observation, we hypothesized that this facilitation (akin to a form of contextual self-prioritization), as restricted to the actionable space, thus serves to enhance the efficiency of actions toward self-owned objects, and likely occurs during action-specific processes.

To test this hypothesis, the following study explored the interaction between ownership and spatial location in online motor inhibition processes, highly involved in supporting efficient actions. We reasoned that if the above-mentioned contextual self-prioritization supports action efficiency, it should manifest not only in faster responses but also in more effective and rapid suppression of erroneous motor activations during interactions with owned versus non-owned objects. To this end, we recorded EMG activity from hand muscles involved in the response. This method also enabled us to observe the different phases of the movement involved in the response, which allowed us to examine whether the facilitation previously observed in RTs emerged during motor execution (or "motor time") or emerged preceding the response execution ("premotor time).

Importantly, as our main purpose was to create a conflict between two information (space and ownership) in order to elicit motor errors (in a manner analogous to interference tasks such as the Stroop task), we first conducted an online experiment comprising (i) an ownership judgement task and (ii) a reachability judgement task, in order to determine which factor was processed first and therefore most likely to influence the other. This preliminary study also allowed us to observe if the pattern of RTs observed in Chapter 4 was replicated online, in different experimental conditions.

# The role of object ownership on online inhibition in peripersonal space

Lucie Lenglart<sup>1,2</sup>, Clémence Roger<sup>1</sup>, Adriana Sampaio<sup>2</sup>, Yann Coello<sup>1</sup>

- 1. Univ. Lille, CNRS, UMR 9193 SCALab Sciences Cognitives et Sciences Affectives, F-59000 Lille, France
- 2. Psychological Neuroscience Lab, Psychology Research Centre (CIPsi), School of Psychology, University of Minho, Braga, Portugal

Key words: Peripersonal space, Object ownership, EMG, Partial error, Motor inhibition

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#### 5.3. Preliminary study: Response time to ownership and reachability judgment

#### 5.3.1. Introduction

A previous study investigating response time during a reachability judgment task (Lenglart et al., 2023) revealed an interaction between ownership and space location (PPS and EPS), supporting the existence of an interference between these two dimensions. However, to observe such interference between two divergent information, one must be more automated – and therefore faster – than the other (Cohen et al., 1990). It is thus required to understand a priori which information is processed faster and determine if the difference in processing speed is statistically significant. In this way, we could confirm the possibility of such interference between the two information and construct the task accordingly.

In a previous experiment, Bartolo et al. (2014a) asked participants to perform three tasks only differing in the instructions given. In one task, they were instructed to estimate if they could reach the stimuli displayed with their right hand if they tried to. In the two other tasks, they were asked to identify the color of the stimuli and their lateral position (left or right). Results showed that the participants were significantly slower to answer in the reachability judgment task than in the pure visual task (color identification) and in the visuo-spatial task (laterality estimation). These results indicate that the processing of the information required to perform the reachability judgment task is slower than that required to perform a pure visual or a simple visuo-spatial task, and should be less automated. In the present main experiment's paradigm, ownership is to be specified through color. In line with the above-mentioned results, one may assume that, in this context, ownership identification is faster than reachability judgment, leading to a specific type of interference. However, as participants were explicitly asked to assess ownership (a conceptual information) and not color, it was necessary to ensure that the identification of a conceptual

#### 5.3.2. Method

information through visual information remained significantly faster than the reachability judgment to enable interference. To this end, we conducted a preliminary study aiming at investigating the relative speed of stimulus processing in an ownership identification task and a reachability judgment task.

## 5.3.2. *Method*

## **Participants**

Nineteen right-handed participants participated in the experiment (14 women, *Mage* = 24.1, SD = 2.9). Sample size was determined with the G\*Power software (version 3.1.9.7). For an alpha level of 0.05, a statistical power of 80%, and a strong effect size considering the result of previous research exploring (Bartolo, 2014), we calculated that a minimum of 15 participants would be needed to perform a two-tailed repeated-measures t-test. All participants were right-handed, had a normal or corrected-to-normal vision, and had no history or neurological or psychiatric conditions. They were recruited online through ads posted on online student forums. Participants received an information letter prior to the experiment and gave their informed consent in accordance with the Declaration of Helsinki (World Medical Association, 2013).

# Materials and apparatus

The task was created on Lab.js builder (Henninger et al., 2020) and hosted online on Pavlovia Surveys (https://pavlovia.org/). The virtual environment and the cups were identical to the ones used in the reachability judgment task with ownership (see the *Method* section of the main experiment). Participants performed a reachability judgment task and an ownership identification task in a counterbalanced order. For each of the two tasks, each coloured cup (blue and yellow) was presented 4 times at 30 distances (ranging from 5 to 145 cm from the proximal edge of the

## 5.3. Preliminary study: Response time to ownership and reachability judgment

virtual table, with an inter-target distance of 10 cm) for a total of 120 trials. After each trial, a mask consisting of a Gaussian blur applied on the virtual environment without any cup present on the table (see Figure 13.B) was presented for 1000ms.

#### **Procedure**

Object ownership was induced at the beginning of the experiment by making the participants choose among the two virtual mugs displayed in the virtual environment. They were then informed that the other cup belonged to the virtual character seated in front of them in the virtual environment. Before starting the experiment, participants were requested to represent themselves seated at the table in the virtual environment and the instructions were displayed on the screen. For the reachability judgment task, participants were asked to estimate whether the cup displayed on the table would be reachable with their right hand or not depending on its location on the table. For the ownership identification task, participants were asked to identify the ownership of the cup displayed on the table. For both tasks, participants were asked to answer as fast as possible, but to try to avoid any mistakes. Responses were provided by pressing the "X" or the "C" response key with the major and the index of the left hand (associated responses randomly attributed for each participant and each task). Participants completed two practice trials before starting each task.

## Data analyses

Data treatment and analysis followed an identical approach to that detailed in the *Data* analyses section of the main experiment. A repeated-measure two-tailed t-test was used to analyse the data.

## 5.3.3. Results and conclusion

## 5.3.3. Results and conclusion

The t-test showed a significant difference between the response time of the reachability judgment task (M = 724.39, SD = 203.79) and the ownership identification task (M = 518.34, SD = 111.14,  $t_{18} = -8.35$ , p < .001). We observed a slower response time for the reachability judgment task than for the ownership identification time (see Figure 12).

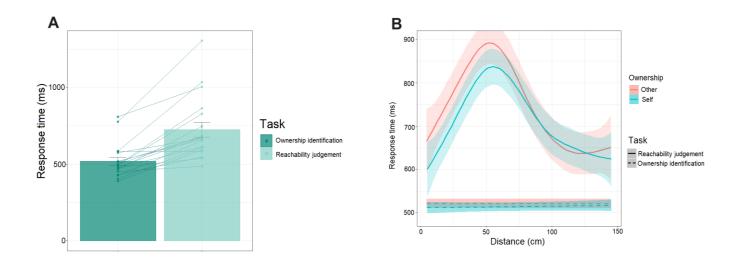


Figure 12. (A) Mean response time and standard error (ms) as a function of the Task. (B) Graphic representation of mean response time through LOESS curve fitting as a function of Task, Ownership and Distance. The two dashed lines represent response times in the ownership identification task while the two plain lines represent response times in the reachability judgment task. The two red lines represent response times when the displayed mug belongs to the virtual character, and the blue lines represent response times when it belongs to the participant. For descriptive purposes, it is interesting to notice that while distance does not seem to affect the Ownership identification, both Ownership and Distance seem to affect the Reachability judgment task.

In this preliminary study, we asked participants to perform a reachability judgment task and an ownership identification task under the same experimental conditions, differing only in the instruction. The results revealed a significant difference between the two response times, with a faster response for ownership identification (206 ms). This difference accounts for a more automated processing of ownership likely to interfere with the processing of information during a reachability judgment task.

# 5.4. MAIN STUDY

## 5.4.1. Abstract

Peripersonal space (PPS), as opposed to extrapersonal space (EPS), refers to the area surrounding the body within which individuals interact with objects or conspecifics. However, objects in PPS can belong to oneself or to others, which was found to influence how these objects are encoded. We analysed the performances of motor responses in a reachability judgment task concerning self-owned and other-owned objects (cups) presented in PPS or EPS. EMG activities were recorded on thumbs (flexor pollicis brevis) to detect correct and erroneous motor activations. Behavioural data showed that motor responses were shorter and longer for self-owned cups compared to other-owned cups in PPS and EPS, respectively. 10% of trials showed initial response errors, which were higher in the EPS for self-owned cups and in the PPS for other-owned cups. 82% of these errors were corrected online, with corrections being more efficient for self-owned cups in the PPS. Overall, the data revealed that reachability judgments were faster and more accurate in the PPS, with more efficient inhibition processes in the presence of motor errors. Motor selection and correction are thus modulated by the social context of object ownership, highlighting the specific role of the PPS in encoding self-relevant objects for action.

#### 5.4.2. Introduction

Reaching, grasping and manipulating objects with the body requires the perceptual segregation of objects that are within reach, i.e. located in the peripersonal space (PPS), from those that are out of reach, i.e. located in the extrapersonal space (EPS; Rizzolatti et al., 1981). The PPS thus represents a near-body action space where we engage in physical interactions with objects or other individuals, using our limbs and other body parts. Originally, the specific nature of PPS originated from single-unit electrophysiological studies in monkeys showing that a set of motorrelated neurons within the ventral premotor cortex, the parietal cortex and the putamen responded more to objects located in the reachable near body space than to objects located in the far out of reach space (Colby et al., 1993; Graziano & Gross, 1993; Graziano et al., 1994; Rizzolatti et al., 1981). From these observations, PPS was conceived as a functional interface between the body and the environment serving the organisation of object-directed motor actions (Brozzoli et al., 2011; Coello & Cartaud, 2021; Graziano & Cooke, 2006; Iachini et al., 2016). Supporting the motor foundations of the PPS, neuroimaging studies highlighted that the mere observation of objects located in the PPS triggered activation in the sensorimotor brain areas (Bartolo et al., 2014b; Chao & Martin, 2000; Culham et al., 2008; Ferri et al., 2015; Grafton et al., 1997; Quinlan & Culham, 2007). Likewise, several studies reported higher motor evoked potentials in the electromyographic signal (Cardellicchio et al., 2011) as well as mu event-related desynchronization in the electroencephalographic signal (Proverbio, 2012; Wamain et al., 2016) when visually encoding objects in the near-body (as compared to far) space, similarly to what was observed during actual objects-directed motor actions (Bestmann & Duque, 2016; Derosiere & Duque, 2020; Pfurtscheller & Neuper, 1994). Moreover, modification of the functional range of motor activities (e.g., through tool-use or limb immobilization), or of the spatial effects of objectdirected actions, has been reported to result in a congruent increase or decrease in PPS (Bourgeois & Coello, 2012; Bourgeois et al., 2014; Leclere et al., 2019; Toussaint et al., 2020). Altogether, these findings support the view that the PPS delimit a near-body space dedicated to the multimodal encoding of visual objects, combining sensory and motor-related information for the purpose of organizing motor behaviours, either in terms of approaching incentive objects or avoiding threatening ones (Coello & Cartaud, 2021; de Vignemont & Iannetti, 2015).

Investigating the multimodal nature of the PPS, a number of studies reported a facilitation effect in the perception of visual objects located in the PPS. For instance, people are faster and more accurate in visual detection and spatial discrimination tasks when the stimuli are located in the PPS (Dufour & Touzalin, 2008; Reed et al., 2006). Other compelling arguments came from the study by Gori et al. (2011), who found enhanced perceptual size discrimination of visual objects inside compared to outside the PPS where perceptual judgments were biased toward underestimation. They also found that the perceptual biases for objects outside the PPS were significantly reduced when sensorimotor calibration mediated by haptic experience of the object was allowed. Other studies revealed also that shape discrimination (Costantini et al., 2010; Spence et al., 2004) or object categorization (Blini et al., 2018) are facilitated when objects are located in the PPS. For instance, Costantini et al. (2010) showed that object-directed arm movements are faster when the imperative visual signal used to trigger the action had a congruent orientation (e.g., using a cup with a handle directed toward the moving arm as a visual stimulus to trigger the action). The perceptual facilitation due to the spatial alignment effect was however observed only for stimuli located in the PPS. Considered together, these data support the view that, in relation with its motor nature, multimodal properties of the PPS contribute to perceptual facilitation. However,

#### 5.4.2. Introduction

a striking aspect of sensorimotor processing of objects in the PPS is that it has been shown to be influenced by objects ownership.

Ownership, defined as a psychological bond between an owner and owned objects manifested by a feeling of *mineness*, has been conceptualized as a specific instantiation of the broader concept of "self-relevance" (or also "self-reference"). The human brain seems indeed highly sensitive to cues associated with the self as we assign particular importance to information, objects, and experiences that are linked to our identity and sense of ownership (Beggan, 1992; Ye & Gawronski, 2016). It has been suggested that this notion of self-relevance could be represented in an "integrative self", a stable self-representation that could be flexibly accessed across different contexts and that could accordingly bound to external information (Scheller & Sui, 2022; Sui & Humphreys, 2015). As such, self-related stimuli are generally processed faster and more accurately than other-related stimuli, and also are subjected to a range of cognitive biases. For instance, information is better remembered when referring to the self (known as the self-reference effect or SRE; Cunningham et al., 2008; Symons & Johnson, 1997). Evidence also supports that selfrelevant information leads to biased orientation and narrowing of attention (Liu et al., 2016; Luck et al., 1994; Sun et al., 2016; Svensson et al., 2023). For Schäfer et al. (2020), the binding of selfrelevant elements would allow the creation of a context-dependent "network of importance" which in turn will influence cognitive processing (context-dependent integrative self, Schäfer et al., 2020). Accordingly, ownership, as a particular instantiation of self-relevance, can orient an individual's perception and interaction with the surrounding environment (Morewedge, 2021).

In accordance with the context-dependent model of integrative self (Schäfer et al., 2020; Sui & Humphreys, 2015), biases related to the processing of self-owned objects are more prone to emerge during direct interaction with the environment, such as goal-directed motor action. As a

matter of fact, in tasks requiring an actual or simulated interaction with tangible objects, self-ownership enables faster motor responses (Constable et al., 2011; Lenglart et al., 2023). Moreover, these effects depend on the spatial location of objects and especially emerge within the PPS, as this space is dedicated to functional interactions between the body and the environment. For instance, Lenglart et al. (2023) asked participants to judge the reachability of self-owned and other-owned objects presented at different distances in a virtual environment. They observed that self-ownership enabled faster processing for self-owned objects, but only when they were located in the PPS. However, the exact nature of the effects of ownership on motor action remains unclear as motor action encompasses a complex interplay of steps involving decision-making for the selection of adapted motor plan (Wolpert & Landy, 2012), as well as the planning, execution, and subsequent monitoring and eventually correction of action to ensure that it corresponds to the intended goal (Barkley, 2012). This ability to ensure that the given response is indeed the one that was decided upon is made possible through cognitive control mechanisms.

Cognitive control, also known as executive control, refers to the set of mental processes and mechanisms that organize the mental life by adjusting information processing to momentary needs in order to enable an individual to achieve specific goals (Hofmann & Kotabe, 2012; Ridderinkhof et al., 2011). It is therefore possible that spatial/ownership manipulations may also affect later stages of information processing, particularly those close to the response under the influence of cognitive control mechanisms (e.g. decision, execution and correction). Interestingly, recent work has demonstrated that self-associated cues facilitated decision making through cognitive control (Svensson et al., 2023). One of the essential mechanisms of cognitive control that enables behaviour to be adjusted in real-time is the ability to inhibit undesirable behaviour. This capacity is essential in numerous life situations where self-control, adaptation to new

#### 5.4.2. Introduction

circumstances, conflict resolution, and inhibition of impulsive behaviours are needed, both in individual and social contexts.

A classic method to evaluate inhibition control involves utilizing EMG recordings through surface electrodes positioned above the relevant muscles engaged in the task's required responses. This methodology enables the detection of the onset of muscle activations and, of greater significance, the observation of tiny muscular activations during the course of the trials (Coles et al., 1985). Therefore, expanding beyond the traditional binary of correct versus incorrect performance, EMG provides the capability to discern additional trial categories. More specifically, EMGs can detect trials in which the correct response was provided but preceded by a small incorrect response that was not strong enough to reach the response threshold. These small incorrect EMG activations, called partial errors, are commonly observed in approximately 15% of incongruent trials within tasks that manipulate stimulus-response congruency (e.g., Burle et al., 2002, 2008; Grisetto et al., 2019). Partial errors are intriguing as they serve as evidence that control monitoring was actively involved. This is because the engaged error was detected, inhibited, and subsequently corrected (Hasbroucq et al., 1999; Roger et al., 2014). The measurement of partial errors is therefore made through metrics evaluating the efficiency of the suppression of incorrect responses following initial activation: first, the correction ratio quantifies the frequency with which erroneous response impulses are corrected, reflecting the proportion of corrected errors among all erroneous responses. To complement this measure, the correction time determines the interval between the initial erroneous response and the subsequent correct response, indicating the duration required to rectify an error.

In this context, the aim of the present study was to improve our understanding of the interaction between ownership and location in space through the study of inhibition control. To

this end, we asked participants to choose for themselves an object (a coloured cup) among two choices and we attributed the other object (a cup with a different color) to a human-like character presented in virtual reality. Participants were then asked to estimate as fast as possible the reachability of self- and other-owned cups presented either in the PPS or EPS, while the EMG activity of the responding muscle fingers was recorded. In relation to the motor properties of PPS, we expected faster reachability judgments as well as more efficient inhibitory mechanisms for self-owned compared to other-owned objects, especially when located in PPS.

## 5.4.3. *Method*

## **Participants**

A total of 30 right-handed voluntary participants (22 women,  $M_{age}$ =21.6, SD =2.9) completed the experiment. The sample size of 30 was determined a priori by means of G\*Power software (version 3.1.9.7). Considering an alpha level of 0.05 and a statistical power of 80%, we calculated that 24 participants would be sufficient to obtain a Cohen's F effect size of 0.25 (i.e., medium effect), estimated on the basis of previous experiments assessing the interaction between the social and conceptual aspects of the environment and the representation of the PPS (Coello & Bonnotte, 2013; Gigliotti et al., 2021; Lenglart et al., 2023). In order to reach this goal, we decided to recruit 30 participants to allow for possible attrition or dropout due to unreliable physiological recordings. All participants were right-handed with a normal or corrected-to-normal vision and had no history of neurological or psychiatric disease. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Participants received an information letter before coming to the experiment site at the University of Lille, and gave their written informed consent prior to the experiment onset. The experimental protocol was conducted in accordance with the ethical

principles of the Declarations of Helsinki (World Medical Association, 2013) and was approved by the University of Lille Institutional Ethics Committee (Ref. No. 2022-634-S109).

## Materials and apparatus

The experimental tasks were created on Octave (version 7.3.0) and conducted on a 27-in. screen (1920\*1080 pixels) located at a distance of 60 cm from the participant, in a closed experimental room. The virtual environment was designed using Unity (version 2021.3.13f1) and included a virtual room with a table (150-cm long) with a 3D texture but no specific spatial cues that would allow the perception of actual distances, at the extremity of which a neutral-faced character taken from the ATHOS database (Cartaud & Coello, 2020) was seated (see Figure 13.A).

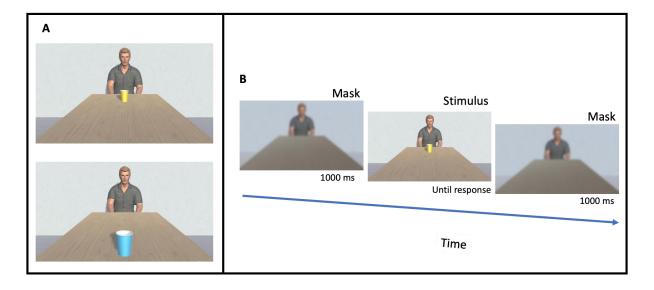


Figure 13. (A) Illustration of the virtual environment with a cup located in the participants' extrapersonal (top panel) or peripersonal space (bottom panel). (B) Time-course of the presentation of the stimuli.

The stimuli consisted of the two virtually replicated cups presented on the table, with one attributed to the participant (self-owned cup) and the other to the virtual character (other-owned cup). Although it would have been interesting to study the effects of the absence of ownership

using neutral objects, it is worth noting that the lack of ownership is a peculiar situation rare in nature (Sherratt & Mesterton-Gibbons, 2015). Indeed, using neutral objects could have caused inconsistencies in the social attribution of neutral objects, as they could be associated with oneself as well as with others depending on contextual factors (Constable et al., 2011; Scorolli et al., 2018). We thus decided not to use neutral objects in the experiment. The two cups were isoluminant in Unity (HSV 100% luminance) and had a similar contrast ratio with the table (blue: table = 1: 6.08; yellow: table = 1: 6.36). A grey cup was also used to estimate the boundary of the PPS. The experimental tasks consisted thus of an initial reachability judgment task with the neutral (grey) cup (i.e., with no ownership), followed by a reachability judgment task with ownership, including self- and other-owned (yellow and blue) cups. A response box was held in both hands, with answer buttons on either side (Figure 14.B). In the initial reachability judgment task, the grey cup was presented at 29 different distances (ranging from 5 to 145 cm from the proximal edge of the virtual table, with an inter-target distance of 5 cm) and a reachability judgment threshold was computed for each participant at the end of the task using the following formula:

$$y = \frac{exp(\alpha + \beta x)}{1 + exp(\alpha + \beta x)}$$

where *x* represents the distance of the cup and *y* represents the participant's probability to estimate the cup as "reachable". The initial reachability judgment task served thus to segment for each participant the table into a PPS and an EPS. In the reachability judgment task with ownership, each of the two-coloured cups was presented at different distances randomly selected along the midline of the table (corresponding to the participants' mid-body sagittal axis), in the PPS (at -70%, -60% or -50% from the previously computed reachability threshold) or in the EPS (at +50%, +60% and +70% from the previously computed the reachability threshold). Filler trials aiming at making the

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task difficult enough were also added, with the cup being presented near the boundary between the PPS and the EPS (at -10%, 0% and +10% of the reachability threshold). For the two reachability judgment tasks, a mask consisting of a Gaussian blur applied to the virtual environment (with no cup on the table, see Figure 13.B) was presented for 1000ms.

Electromyographic activities (EMG) were recorded using Ag/AgCl electrodes with the BioSemi© system (BioSemi ActiveTwo electrodes, Amsterdam). EMG in the left and right hands was recorded to detect partial errors and the onset of any muscular burst. To this end, two pairs of electrodes were placed on the surface of the skin above the thumb, on the *flexor pollicis brevis* muscle and were spaced approximately 2 cm apart (see Figure 14.A). The sampling rate was set at 1024 Hz.

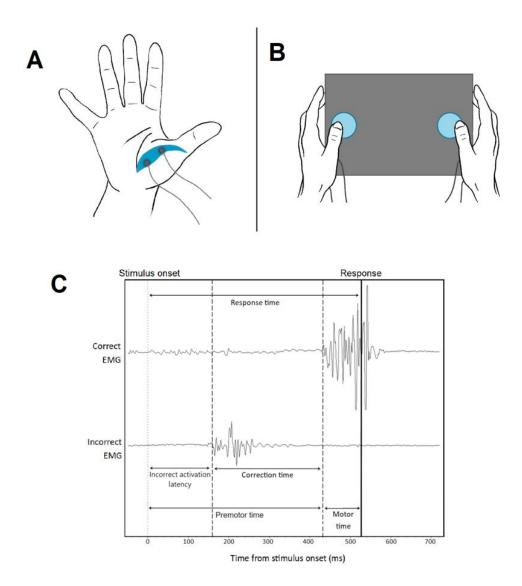


Figure 14. (A) Schematic illustration of the EMG placements. The electrodes were placed at the surface of the skin, on the flexor pollicis brevis (in blue). (B) Schematic illustration of the response box. The box was placed on the table so that the arms and hands of the participants, placed on each side of the box, could fully rest on the table. (C) Example of a typical correct trial containing a partial error. Correct and incorrect EMG signals as a function of the expected response are respectively presented in the upper part and lower part of the panel. Response time corresponds to the time between the stimulus onset and the response recorded by the device. Incorrect activation latency represents the time between the stimulus onset and the incorrect activation onset. Correction time corresponds to the time between the partial error EMG onset and the EMG onset of the correct response. The Premotor time (not analysed here) is constituted of the

#### 5.4.3. Method

Incorrect activation latency and of the correction time, and the Motor time (MT) corresponds to the time between the EMG onset of the correct response and the effective response.

At the end of the experiment, participants were requested to answer a questionnaire composed of two questions relating to object ownership ("How much did you feel that the cup that you have chosen belonged to you?"; "How much did you feel that the other cup belonged to the virtual character") on a Likert scale ranging from 0 ("Not at all") to 7 ("Completely"). Answering "0" to both questions was considered an exclusion criterion, leading to the participant's rejection.

## **Procedure**

Preliminary study. The purpose of the main experiment was to better understand the interaction between object ownership and object location in space (especially in PPS) in cognitive control subtending motor action. Such interaction is usually brought about by the interference of one information over the other. In order to ensure the possibility of such interference and orient the instructions accordingly, it was necessary to investigate the relative processing speed of information involved in the identification of ownership and of that involved in the reachability judgment. To do so, we conducted a preliminary online study with the aim of comparing the response time of participants in an ownership identification task and in a reachability judgment task (see supplementary material). On average, the identification of ownership was 206 ms faster than reachability judgment. Since results pointed toward a significantly faster - and thus more automated - processing of ownership (Cohen et al., 1990), this suggests that objects processing is more likely to initiate interference if participants are instructed to perform a reachability judgment. It's important to highlight that the preliminary study had some differences from the main study. Notably, it was conducted online rather than onsite, and participants were instructed to prioritize the speed-accuracy trade-off as opposed to responding as quickly as possible in the main study. As

a result, the reachability judgment task was on average slower in the preliminary study than in the main study.

Main study. On arrival at the experiment site, the participants signed the informed consent and had to choose one among two cups (yellow or blue) in order to induce object ownership. Among the participants, 44% chose the yellow cup, and 56% chose the blue cup. The participants were told that the chosen cup was now theirs, and that as the experiment was a little long, they could use it at any time to drink water if they needed to. Then the EMG electrodes were placed and the participants were seated in front of the computer screen showing the virtual room with the response box held by both hands. They were asked to represent themselves as if they were at the proximal edge of the table located in the virtual room. The participants then performed successively the initial reachability judgment task (grey cup) and the reachability judgment task with ownership (self- and other-owned cups). At the beginning of each task, participants were instructed to perform the task as fast as possible, but without making too many errors.

Initial reachability judgment task. In the initial reachability judgment task, participants were asked to estimate if they could reach the virtual cup displayed on the table with their right hand without moving their trunk or their shoulders. The cup displayed was a neutral grey cup, and no statement was made about its ownership. The participants provided the responses by using a response box and pressing the left button with their left thumb if the cup was reachable or by pressing the right button with their right thumb if the cup was not reachable (the response button was counterbalanced across participants). The cup was presented four times at each of the 29 distances for a total of 116 trials (29 distances × 2 repetitions). Between each trial, the blurred mask was presented for 1000 ms (see Figure 13.B).

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Reachability judgment task with ownership. Before the onset of the reachability judgment task, the experimenter asked the participants to remind her which cup they owned. To illustrate the ascription of ownership, a picture representing the cup of the participants near themselves and the other cup near the virtual character was displayed while the experimenter recalled that the non-chosen cup was attributed to the virtual character. The instructions given to the participants were exactly the same as in the initial reachability judgment task, except that they were explicitly asked to estimate the reachability of the two-coloured cups from their own perspective to avoid any confusion. The task was composed of 7 experimental blocks. In each block, the two cups were presented eight times at each distance within the PPS and EPS. In order to add difficulty to the task, 24 non-analysed filler trials were included in the task, where each of the two cups appeared 12 times near the boundary of the PPS. In total, each block consisted of 120 trials (2 spaces × 3 distances × 2 colours × 8 repetitions + 24 fillers). In total, the experiment lasted approximately one hour.

# Data acquisition and pre-processing

The EMG data were filtered with a 10 Hz high-pass filtering. Onsets of EMG activities were detected manually through visual inspection (Staude et al., 2001; van Boxtel et al., 1993). The experimenter who analysed the data was not aware of the trial selected. Trials were then classified into three categories: (1) pure-correct trials, characterized by a single muscular burst on the correct side, (2) full error trials, characterized by a single muscular burst on the incorrect side, and (3) partial error trials, characterized by a muscular burst on the incorrect side followed by a correct response (see Figure 14.C). Trials that did not align with any of the three categories, representing 7% of the test trials, were excluded from the analysis.

## Data analysis

Some trials, by carrying conflicting information, can be more prone than others to give rise to errors. This propensity was evaluated by computing the rate of initiated errors (i.e. incorrect activations) among all trials. To do so, we computed the total of trials involving an erroneous activation by summing the number of partial errors to the number of full errors. The number of initiated errors was then divided by the total number of trials. We then estimated the efficiency of inhibition control through the correction ratio, that is the proportion of errors that were corrected in time. This ratio was computed by dividing the number of partial errors (which were corrected) by the number of initiated errors (partial errors and full errors). This measure was chosen over that of the absolute number of partial errors, as the latter would be less relevant because it would blend the vulnerability to stimulus capture with the effect of inhibition mechanisms. Therefore, it is recommended to analyse the proportion of incorrect activations, encompassing all initiated errors (both corrected and uncorrected) separately from the proportion of partial errors among the incorrect activations (Burle et al., 2002). Then, for the trials with partial errors, we reported the latency of the incorrect activation of the partial error and computed the correction time (i.e. the time needed to correct the erroneous response into a correct response) by subtracting the onset of the erroneous burst from the onset of the corrective burst response (see Figure 14.C). We also reported the voltage of the rectified peaks corresponding to the maximum amplitude of the incorrect EMG burst 5 ms around the peak (Klawohn et al., 2020; Liesefeld, 2018) in order to obtain an estimation of the magnitude of the muscle force elicited by the partial errors (Bouisset & Maton, 1972; Leonard et al., 2004). We completed the analysis by calculating the motor time (MT) for both pure-correct and partial errors by subtracting the onset of the correct EMG burst from the response time. Finally, for exploratory purposes, a Conditional Accuracy Function (CAF)

was performed to explore the strength of the alternative response capture over all trials. The likelihood that the first burst of a trial was erroneous was computed as a function of time using the "dmcfun" package (MacKenzie et al., 2024; for a more detailed description of the CAF calculation, see Ulrich et al., 2015). More precisely, the latency of the first bursts was vincentized (Vincent, 1912) and then divided into five bins of equal number of observations (i.e., quintiles). The slope of the first segment of the CAF was then calculated, as it is known to index the strength of the initial activation of the alternative response (Ridderinkhof, 2002b).

The frequentist analyses were performed on R version 4.2.2 (R Core Team, 2022) using the car (Fox & Weisberg, 2019) and the stats (R Core Team, 2022) packages. We used a 2 Ownership (self-owned, other-owned) × 2 Spaces (PPS, EPS) repeated-measures ANOVA to analyse the data. As the residuals of the models did not follow a normal distribution, a Box-Cox transformation for linear models (Box & Cox, 1964) was applied to the data using the following formula:

$$y(\lambda) = \frac{y^{\lambda} - 1}{\lambda}$$

where the optimal  $\lambda$  was estimated with the *boxcox* function of the MASS R package (Ripley et al., 2013). Effect sizes were determined with partial eta-squared ( $\eta^2$ ) and post-hoc comparisons of the significant effects were corrected following the Bonferroni method (Bonferroni, 1936). The box-cox transformation did not allow for the achievement of the normality of residuals for the measure of peaks; in this case, Friedman ANOVA (Friedman, 1937) and Wilcoxon signed-rank tests (Wilcoxon, 1945) were conducted on the non-transformed data. For all analyses, the alpha level was set at 0.05.

Bayesian analyses were also conducted in order to overcome the limitations of the frequentist approach regarding the testing of the null hypothesis (Dienes, 2014; Rosenfeld & Olson, 2021; Rouder et al., 2009). Indeed, when obtaining non-significant results between conditions with the frequentist approach, the use of Bayesian analyses could provide evidence for no difference and bring additional information for the interpretation of null results. In Bayesian analyses, the likelihood of a particular model over the likelihood of another particular model is given through the Bayes factor. The Bayes factor in favour of H0 (BF<sub>01</sub>) indicates the likelihood of the null model over the likelihood of the alternative model. The null model always has a BF<sub>01</sub> of 1; for the other model, a BF<sub>01</sub> above 1 supports the null hypothesis, and a BF<sub>01</sub> below 1 supports the alternative hypothesis (Dienes, 2014; Jeffreys, 1961). Thus, when non-significant data were obtained, we performed a corresponding (ANOVA or t-test) Bayesian analysis and reported BF<sub>01</sub> values. Bayes analyses were performed on Jamovi version 2.3.21, with default values.

## 5.4.4. Results

## Behavioral analysis

Overall, in all trial categories, the mean response time (RT) was 491.68 ms (SD = 108.50). Statistical analysis showed a main effect of Space on RT ( $F_{(1,28)} = 47.56$ , p < .001,  $\eta^2_p = .63$ ). Faster responses were obtained in the PPS (M = 465.84, SD = 98.34) than in the EPS (M = 517.43, SD = 112.80,  $t_{(28)} = 6.89$ , p < .001). No main effect of Ownership was found ( $F_{(1,28)} = 0.041$ , p = .84,  $BF_{01} = 0.63$ ). However, results revealed a significant Space × Ownership interaction ( $F_{(1,28)} = 25.59$ , p < .001,  $\eta^2_p = .48$ ). Post-hoc comparisons revealed that, in the PPS, mean RT was shorter for self-owned cups compared to other-owned cups (self-owned: M = 457.45, SD = 95.04; other-owned: M = 474.23, SD = 102.50;  $t_{(28)} = 3.96$ , p = .001). Conversely, RT was shorter for other-

#### 5.4.4. Results

owned cups compared to self-owned cups in the EPS (other-owned: M = 509.57, SD = 107.50; self-owned: M = 525.28, SD = 119.25;  $t_{(28)} = -3.85$ , p = .002, Figure 15).

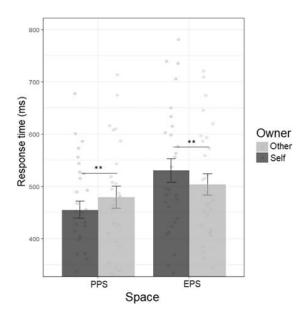


Figure 15. Mean response time and standard error (ms) as a function of Space (PPS, EPS) and Ownership (self-owned, other-owned).

## EMG analysis

The results obtained in the behavioral global analysis are consistent with the literature; therefore, the analysis of the EMG recordings enables a deeper understanding of the mechanisms underpinning the observed behaviours. Based on the EMG recordings, 89.6%, 8.3% and 2.1% of trials were pure-correct, partial error and full error trials, respectively.

## Pure-correct trials

Statistical analysis of the pure-correct trials showed that the onsets of the muscular activity were significantly influenced by Space ( $F_{(1,28)} = 57.00$ , p < .001,  $\eta^2_p = .67$ ). Pairwise comparison showed that the correct responses were initiated faster for the cups located in the PPS (M = 282.48,

SD = 62.66) than for those located in the EPS (M = 326.65, SD = 75.14,  $t_{(28)} = 7.59$ , p < .001). No main effect of Ownership was found ( $F_{(1,28)} = 2.78$ , p = .106,  $BF_{01} = 4.51$ ). The analysis also revealed a significant Space × Ownership interaction ( $F_{(1,28)} = 24.73$ , p < .001,  $\eta^2_p = .47$ ). Posthoc analysis showed that onsets were shorter for self-owned cups compared to other-owned cups in the PPS (self-owned: M = 276.14, SD = 62.40; other-owned: M = 288.82, SD = 63.36;  $t_{(28)} = 4.01$ , p = .002). Conversely, onsets were shorter for other-owned cups compared to self-owned cups in the EPS (other-owned: M = 321.15, SD = 69.36; self-owned: M = 332.16, SD = 81.35;  $t_{(28)} = -3.27$ , p = .011).

No effect was found on motor execution: MT was not impacted by Space ( $F_{(1,28)} = 0.24$ , p = .628,  $BF_{01} = 3.64$ ) nor by Ownership ( $F_{(1,28)} = 4.02$ , p = .055,  $BF_{01} = 3.69$ ). No Space × Ownership interaction was observed ( $F_{(1,28)} = 3.60$ , p = .069,  $BF_{01} = 44.35$ ). In addition, no difference in the intensity of the muscular response was found in correct trials: the Friedman ANOVA did not find any significant effect of Space or Ownership on EMG Peak size ( $\chi 2(3) = 0.543$ , p = .909, Figure 16). Bayesian analysis provided additional evidence for the absence of effect of Space (z = 206; p = 0.815;  $BF_{01} = 4.54$ ) and Ownership (z = 231; p = 0.782;  $BF_{01} = 5.03$ ), as well as for the absence of Space × Ownership interaction ( $BF_{01} = 83.34$ ).

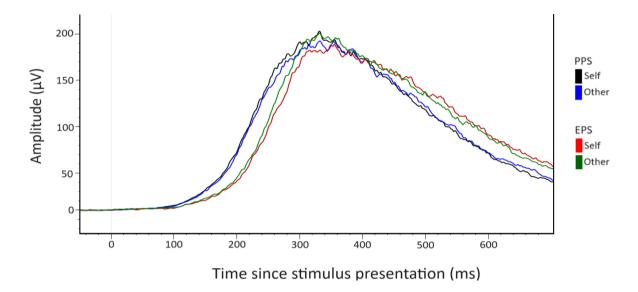


Figure 16. Grand Average of the EMG responses for Pure-Correct trials as a function of Space (PPS, EPS) and Ownership (self-owned, other-owned).

## Incorrect EMG activations

The incorrect EMG activations were observed in situations where errors were initiated, namely, in trials where a partial error occurred before the correct response, and full error (uncorrected) trials. On average, participants-initiated errors on 10% of the trials (SD = 7.48). The ANOVA showed no significant effect of Space ( $F_{(1,28)} = 1.72$ , p = .201,  $BF_{01} = 2.08$ ) nor Ownership ( $F_{(1,28)} = 1.22$ , p = .279,  $BF_{01} = 5.52$ ) on the initiated error rate. A significant interaction was found between Space and Ownership ( $F_{(1,28)} = 19.76$ , p < .001,  $\eta^2_p = .41$ , Figure 17.A). With respect to space, more errors were initiated for the incongruent cups, i.e., when the self-owned cups where located in the EPS (self-owned: M = 10.14%, SD = 5.63; other-owned: M = 7.02%, SD = 5.48;  $t_{(28)} = -4.69$ , p < .001) and when the other-owned cups were located in the PPS (other-owned: M = 12.39, SD = 8.17; self-owned: M = 10.31, SD = 9.26;  $t_{(28)} = 2.92$ , p = .027, see Figure 17.D for individual data).

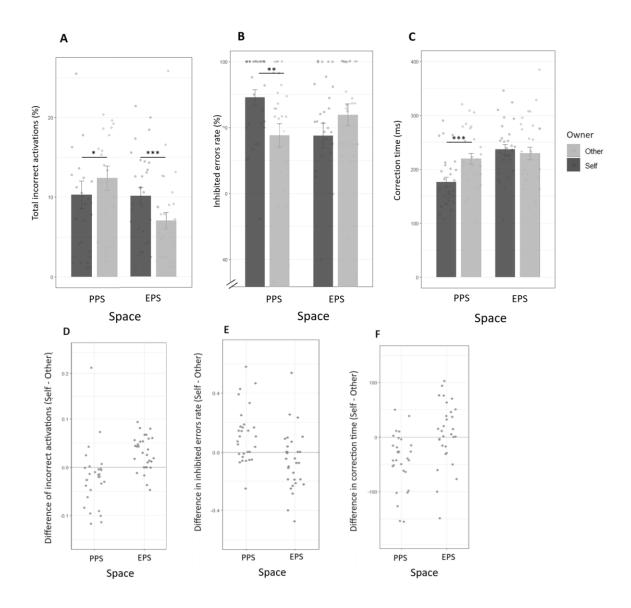


Figure 17. (A) Mean total incorrect activations (%), (B) mean inhibited error rate (%) and (C) mean correction time (ms) as a function of Space (PPS, EPS) and Ownership (self-owned, other-owned). Error bars represent standard error. Strip charts represent the individual differences between the results for Self-owned and Other-owned cups considering (D) incorrect activations, (E) mean inhibited error rate and (F) mean correction time, in PPS and EPS respectively.

#### 5.4.4. Results

The improvement in accuracy for rapid errors was consistent across conditions: the slope between the first two quintiles of the CAF revealed no effect of Space (F(1,28) = 0.01, p = 0.983,  $BF_{01} = 5.15$ ), of Ownership ( $F_{(1.28)} = 0.325$ , p = 0.573,  $BF_{01} = 4.91$ ), and no interaction effect between Space and Ownership ( $F_{(1,28)} = 1.381$ , p = 0.250,  $BF_{0l} = 72.93$ ). As accuracy rates increased similarly across conditions for rapid errors, these results indicate that the effects aforementioned are likely not imputable to impulsivity. Indeed, the plot of the CAF (see Figure 18) seems to depict a persistent difference between the congruent (i.e., self-owned object in PPS and other-owned object in EPS) and incongruent (i.e., other-owned object in PPS and self-owned object in EPS) conditions. We thus computed the delta values for accuracy of the congruent versus incongruent condition in PPS (Other - Self) and EPS (Self - Other) in order to observe the magnitude of interference effects as a function of response speed (Ridderinkhof, 2002a). We then performed a 2 Spaces \* 5 Quintiles repeated-measures Friedman ANOVA on these delta values. The results showed a difference between the conditions ( $\chi 2_{(9)} = 62.3$ , p < .001) caused by an effect of the Quintile ( $\chi 2_{(4)} = 48.9$ , p < .001). Specifically, starting from the second quintile, the delta of each quintile was of higher value than that of the preceding one (all p < .034). However, no effects of Space ( $\chi 2_{(1)} = 0.310$ , p = .577,  $BF_{0I} = 7.89$ ) and no interaction effect between Space and Quintile  $(BF_{01} = 33.11)$  were observed.

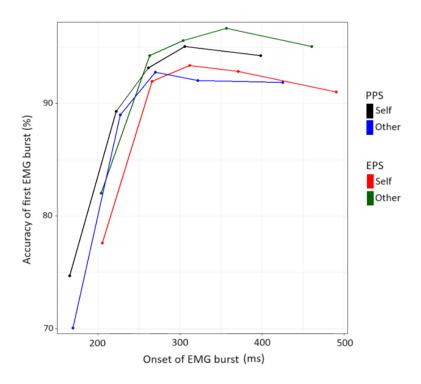


Figure 18. Conditional accuracy function (CAF) presenting accuracy of the first EMG burst as a function of space (PPS, EPS), ownership (Self, Other) and time (ms). Each point on the x-axis corresponds to the midpoint of each quintile.

## Partial errors

Among the incorrect activations, participants corrected 82% of initiated errors on average (SD=18.16), which corresponds to the correction ratio (i.e. the ratio of partial errors). No main effect of Space  $(F_{(1,28)}=0.75, p=.394, BF_{0l}=4.77)$  nor Ownership  $(F_{(1,28)}=0.76, p=.390, BF_{0l}=4.63)$  was found. A significant interaction effect was found between Space and Ownership  $(F_{(1,28)}=19.51, p<.001, \eta^2_p=.41$ , Figure 17.B). Post-hoc comparisons revealed that in the PPS, self-owned cups (M=89.10, SD=13.04) were more likely to be inhibited than other-owned cups  $(M=77.62, SD=18.90, t_{(28)}=-3.37, p=.009)$ . In the EPS, no difference was found between

other-owned cups (M = 83.86, SD = 17.68) and self-owned cups (M = 77.52, SD = 20.42;  $t_{(28)} = 1.57$ , p = .510,  $BF_{01} = 1.77$ , see Figure 17.E for individual data).

Incorrect activations related to the partial errors showed delayed latencies impacted by Space  $(F_{(1,28)} = 17.06, p < .001, \eta^2_p = .38)$ : the participants initiated the erroneous activation faster in the PPS (M = 4.99, SD = 1.52) than in the EPS  $(M = 5.17, SD = 1.41, t_{(28)} = -4.13, p < .001)$ . The latency of the incorrect activation was therefore not impacted by Ownership  $(F_{(1,28)} = 1.52, p)$ = 0.228,  $BF_{01}$  = 3.31) and no effect of Space × Ownership was observed  $F_{(1,28)}$  = 1.64, p = 0.210,  $BF_{01} = 1.71$ ). The analysis of the correction time of partial errors showed a main effect of Space  $(F_{(1,28)} = 25.57, p < .001, \eta_p^2 = .47, \text{ Figure 17.C})$ . The observed effect was due to faster corrections when the cups were located in the PPS (M = 197.89 ms, SD = 55.24) than in the EPS (M = 232.99,  $SD = 57.85, t_{(28)} = 5.31, p < .001$ ). A main effect of Ownership was also found  $(F_{(1,28)} = 6.74, p =$ .015,  $\eta_p^2 = .19$ ). Indeed, faster corrections were observed for self-owned cups (M = 206.51, SD =57.93) than for other-owned cups  $(M = 224.37, SD = 59.21, t_{(28)} = 3.01, p = .005)$ . In addition, a Space × Ownership interaction was observed ( $F_{(1,28)} = 15.10$ , p < .001,  $\eta^2_p = .35$ ). Specifically, faster corrections were observed for self-owned cups compared to other-owned cups, but only in the PPS (self-owned: M = 176.30, SD = 48.55, other-owned: M = 219.47, SD = 53.75,  $t_{(28)} = 4.89$ , p = .001, Figure 18). In the EPS, no difference was found between self-owned cups and otherowned cups (self-owned: M = 236.72, SD = 50.85; other-owned: M = 229.26, SD = 64.80;  $t_{(28)} =$ -0.46, p = 1,  $BF_{01} = 4.59$ ). Finally, the MT was not impacted by Space ( $F_{(1,28)} = 0.067$ , p = .797,  $BF_{01} = 4.86$ ) nor by Ownership  $(F_{(1.28)} = 1.72, p = .20, BF_{01} = 3.34)$ . No Space × Ownership interaction was observed ( $F_{(1,28)} = 2.12$ , p = .156,  $BF_{01} = 29.48$ , see Figure 17.F for individual data).

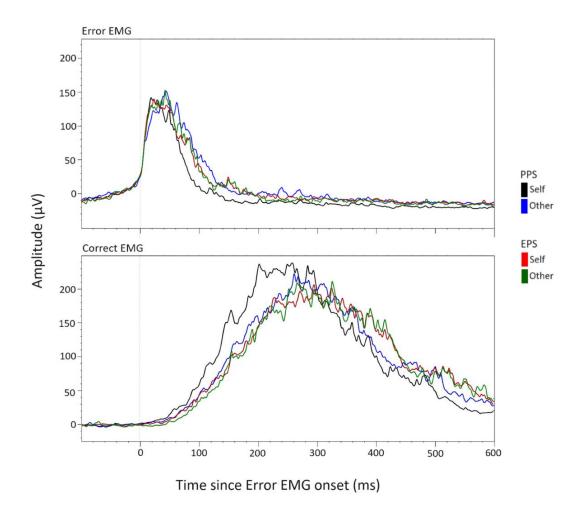


Figure 19. Grand Average of the EMG responses for partial errors as a function of Space (PPS, EPS) and Ownership (self-owned, other-owned).

The effect found on correction time was not related to a difference in the strength of the incorrect burst: overall, the Friedman ANOVA did not find any significant effect of Space or Ownership on EMG Peaks size ( $\chi 2(3) = 3.72$ , p = .294). Specifically, Bayesian analysis supported the absence of effect of Space (z = 221; p = 0.949;  $BF_{01} = 4.30$ ) and Ownership (z = 180; p = 0.429;  $BF_{01} = 4.16$ ), as well as the absence of Space × Ownership interaction ( $BF_{01} = 26.01$ ).

#### 5.4.5. Discussion

The present study focused on the effect of ownership and space on cognitive control subtending motor action. Specifically, we investigated behavioral and EMG performances related to reachability judgements of self-owned and other-owned objects presented in either PPS or EPS using a virtual environment. In relation to the motor properties of PPS, we expected faster reachability judgments, as well as more efficient inhibition of initiated errors for self-owned compared to other-owned objects when located in PPS.

In agreement with our expectations, we observed that the time required to judge reachability was faster for self-owned objects compared to other-owned objects, in particular in the PPS. Indeed, reachability judgments for self-owned cups compared to other-owned cups were 23 ms shorter in the PPS and 29 ms longer in the EPS. This result was associated with the fact that ownership judgment was on average 206 ms faster than reachability judgment (see the preliminary study in the Supplementary material), which may account for the interference effect observed between ownership and spatial location in the reachability judgment task. This result confirms previous studies that have highlighted an effect of ownership in the processing of objects located in the PPS (Constable et al., 2011; Lenglart et al., 2023). It is however worth noting that the same outcome was obtained in the present study despite the use of higher time constraints, as motor responses were provided by participants as fast as possible, highlighting the robustness of the effect previously reported. In addition, the advantage of self-owned objects compared to other-owned objects observed in the PPS inverted in the EPS. The observed effect in EPS, which was not found in previous studies (Lenglart et al., 2023), might be related to the quality of the realism of the virtual agent. Indeed, the virtual agent used in the present study was breathing and produced eye blinking, which is known to enhance the feeling of social presence (Tanenbaum et al., 2014). This

interpretation is furthermore in line with previous research that showed a mirror-like effect of ownership on response time in the EPS in the presence of a human co-actor (Patané et al., 2021).

Echoing the differences in RT, the rate of initiated response errors was also influenced by space and ownership. Overall, 10% of trials showed initiated response errors on average, which were higher for self-owned cups in the EPS (+3%) and for other-owned cups in the PPS (+3%). These effects cannot be imputed to a difference in the size of the partial errors' bursts. These contrasted effects can be rather accounted for by the fact that ownership processing was faster than reachability judgments, and may thus interfere with the reachability decisions. Accordingly, responding reachable for objects in PPS may have been facilitated by the prior identification of self-owned objects (congruent condition), and conversely responding unreachable for objects in PPS may have been altered (incongruent condition) by the prior identification of self-owned objects. Interestingly, the observed effects mimic with ownership information what has been observed in other tasks manipulating spatial stimulus-response congruency, like the Simon effect for instance (Simon & Rudell, 1967). It is worth noting that the analysis of the CAF remarkably showed that the difference between congruent and incongruent trials in the rate of initiated response errors increased over time, depicting a persistent interaction between space and ownership. This could be explained by the fact that cues conveying strong social constructs, such as the social norms referring to property, constitute persistent information difficult to disregard.

Remarkably, 82% of initiated errors were corrected during the trials. This highlights that a substantial majority of these errors were promptly detected, inhibited and corrected. This efficiency was manifestly made possible thanks to highly effective cognitive control mechanisms, notably monitoring and inhibition. However, the results of the present study demonstrated that inhibition efficiency can be influenced by ownership and the spatial context of object presentation.

In particular, when participants-initiated errors while dealing with self-owned cups within the PPS, they showed a significantly higher correction ratio (12%) and executed corrections with significantly greater speed (43 ms), compared to their responses with other-owned cups. Furthermore, no effect was observed on MT, which reflects the speed of voluntary muscle contraction (Hasbroucq et al., 2013). This suggests that the effect observed likely originated at a premotor level rather than being attributable to changes in peripheral motor processes. These findings indicate that even though errors toward PPS were initiated faster than those toward EPS, inhibition operated with greater efficiency and were more effectively mobilized objects situated within the PPS. They are also in line with previous research that has consistently shown faster processing (Blini et al., 2018; Costantini et al., 2010; ter Horst et al., 2011) and greater accuracy (Gori et al., 2011) when dealing with manipulable objects located in the PPS. The present study adds, however, that the cognitive control underlying efficient motor responses in the PPS depends on object ownership.

Overall, the present findings underline the important contribution of implicit space and ownership representations in object-directed motor control. They indicate that when a task is executed under strict temporal or attentional constraint, information is processed in relation to a priority map (Todd & Manaligod, 2018), that integrates spatial (Costantini et al., 2010) and ownership information (Golubickis et al., 2021). In accordance with this priority map, behavioral decisions were faster and more accurate for self-owned compared to other-owned cups, and motor errors were corrected faster and more frequently, although only in the PPS. These findings underline that PPS represents a major constraint in this priority map, being attributable to its role as a motor interface between the body and the self-relevant environment (Brozzoli et al., 2011; Coello & Cartaud, 2021; Iachini et al., 2016). They also underline that the priority map depends

on the context-sensitive "integrative self" (Schäfer et al., 2020; Sui & Humphreys, 2015), which interferes with objects processing in the PPS in order to facilitate perceptual decision-making in resource-constrained contexts. Thus, these findings add to the previous literature that has underlined perceptual facilitation in the PPS (Blini et al., 2018; Costantini et al., 2010; Gori et al., 2011; ter Horst et al., 2011), by showing that cognitive control, in relation to self-owned objects, is also more efficient in the PPS.

The study of neural mechanisms underpinning these results would offer an interesting line of research. Indeed, response inhibition involves multiple neural regions including fronto-parietal and cingulo-opercular networks (Swick et al., 2011; Zhang et al., 2017). How these networks interact with the fronto-parietal network underlying the processing objects in the PPS (Bartolo et al., 2014b; Cléry et al., 2018) and with areas crucially involved in the processing of ownership, such as the ventro-medial prefrontal cortex (vmPFC, Lockwood et al., 2018; Turk et al., 2011), represents a key challenge for forthcoming studies. In this context, the role of the right inferior frontal gyrus (rIFG) is particularly interesting given its major role in inhibition processes (Banich & Depue, 2015; Sagaspe et al., 2011). Notably, the rIFG may manage relevant information for cognitive control, such as social (Sagaspe et al., 2011) or action-relevant information (El-Sourani et al., 2018), serving as a pivotal hub for integrating contextually relevant cues for motor action (Banich & Depue., 2015). In this sense, as ownership conveys key social information (Scorolli et al., 2018; Turk et al., 2011), it could have a particular impact on cognitive control through the functional connectivity between rIFG, vmPFC and pre-SMA (Hare et al., 2009, 2010; Yu et al., 2015).

In conclusion, the present study showed that the manipulation of space and ownership as experimental factors can influence high-level processes such as cognitive control. In particular,

#### 5.4.5. Discussion

higher performances in the PPS for self-owned objects and in the EPS for other-owned objects were observed. In addition, inhibition processes following ownership-dependent decision errors were more efficient in the PPS. This underlines the specific role of the PPS in encoding selfrelevant objects for action. The present study also demonstrated the utility of using EMG to gain a deeper understanding of high-level cognitive processes, particularly inhibition, in the context of investigating action selection mechanisms toward objects, based on social characteristics, particularly ownership. It is noteworthy that the inhibition mechanisms reported in the current study are close to the one described in classic motor inhibition tasks such as Go/No-Go or Stop Signal Tasks (Aron, 2007; Coxon et al., 2006; Raud et al., 2022). However, an important difference is that these paradigms rely on externally triggered inhibition. In the absence of any external stimuli triggering inhibition, our paradigm focuses on internally generated inhibition, which requires the participant to take into account the context. Since the processes underlying internally-generated and externally-triggered inhibition are not completely identical (Parkinson & Haggard, 2015; Schel et al., 2014), it would be interesting, in future studies, to investigate the interaction between self-ownership and peripersonal space in tasks focusing on externally-triggered inhibition. Followup studies would also be necessary to decipher the contribution of the different factors involved in the cognitive control underlying motor performances, such as the emotional context of self and other representations for instance. Importantly, the inhibition process highlighted in the present study in relation to space and ownership could provide a new framework for testing pathological populations, in particular those showing specific executive function or social deficits.

#### **Authors contribution**

L.L. C.R. and Y.C established the research questions and design. L.L. developed the tasks in virtual reality, and collected and analysed the data. All authors contributed to the writing of the manuscript.

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#### 6. OBJECT OWNERSHIP PROCESSING IN PERIPERSONAL SPACE: AN EEG STUDY

#### 6.1. Foreword

In Chapters 4 and 5, we characterized the interaction between object ownership and spatial location. We showed that the prioritization of self-owned objects was contextual and contingent on the object location within the actionable PPS. We further observed that inhibition control was enhanced for self-owned objects in the PPS, suggesting that self-ownership optimized action selection and correction mechanisms in PPS. Interestingly, in some cases, a reverse prioritization pattern emerged, where RTs were shorter for other-owned objects in EPS. These findings clearly highlight an interaction between spatial location and ownership; however, how and when these two factors interact in object's processing remains unclear. Does this interplay appear at one moment in time, potentially reflecting an emergence from a single mechanism, or does it reflect the sequential influence of different mechanism emerging at distinct stages of the processing stream?

To address this, the following study used EEG to investigate the temporal dynamics of this interaction during a reachability judgement task. Given that both PPS encoding and self-prioritization have been associated with early perceptual mechanisms (as reflected in ERP components such as the N1), and later decisional processes (as reflected by the P3), we examined a range of ERP possibly modulated by both space and ownership to track when and how these two factors modulate stimulus processing.

## Object ownership processing in peripersonal space: An EEG study

Lenglart, L.<sup>1,2,3</sup>, Roger, C.<sup>1,2</sup>, Sampaio, A.<sup>3</sup>, Coello, Y.<sup>1,2</sup>

- 1. Univ. Lille, CNRS, UMR 9193 SCALab Sciences Cognitives et Sciences Affectives, F-59000 Lille, France
- 2. Univ. Lille, CNRS, FR 2052 SCV Sciences et Cultures du Visuel, F-59200 Tourcoing, France
- 3. Psychological Neuroscience Lab, Psychology Research Centre (CIPsi), School of Psychology, University of Minho, Braga, Portugal

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#### 6.2.1. Abstract

A fundamental aspect of interacting with objects in the environment is the ability to distinguish between objects that can be directly acted upon in the peripersonal space (PPS) and those out of immediate reach in the extrapersonal space (EPS). Performing appropriate actions also requires integrating social conceptual information related to who owns a particular object. While prior research has demonstrated that spatial and social factors influence object processing, how these factors are integrated is not vet fully understood. To address this issue, the present study explored the neurophysiological correlates of object ownership processing when objects were located in either the PPS or EPS. Facing a virtual character, 28 participants estimated the reachability of self-owned or other-owned objects, placed at different distances. The analysis confirmed that self-owned objects are processed faster when located in PPS, and other-owned objects when located in EPS. EEG signals analysis revealed that early event-related potential components, such as the N1 and anterior N2, were modulated solely by objects' spatial location. In contrast, later components, including the P3 and anterior N400, were influenced by object ownership, although depending on object's location in space. These results suggest an early perceptual prioritization of objects in the PPS, and a prioritization of objects that engages the self at a post-perceptual stage. Overall, the findings provide new insights into how objects are processed depending on their spatial and social properties, and confirm that virtual reality represents a promising tool to probe neural mechanisms supporting perception and action in social contexts.

#### 6.2.2. Introduction

Peripersonal space (PPS) refers to the area immediately surrounding the body, where objects and sensory stimuli can be interacted with and perceived as having a direct influence on one's own actions and safety (de Vignemont et al., 2021). This spatial region is not rigidly defined but is rather flexible and modulated by numerous factors, including body characteristics (Leclere et al., 2019; Toussaint et al., 2020), environmental constraints (Morgado et al., 2013), emotional content (Cartaud et al., 2018; Morgado et al., 2011), and social context (Gigliotti et al., 2021). The brain's ability to continuously monitor PPS is essential for activities like reaching and grasping objects, avoiding obstacles, and responding to potential threats (de Vignemont & Farnè, 2024; Graziano & Cooke, 2006). Neural studies in humans and non-human primates have identified specific brain regions involved in encoding PPS, including the parietal cortex, the premotor cortex and the insula (Bartolo et al., 2014b; Cléry et al., 2015; see Grivaz et al., 2017 for a review). These regions contain neurons that respond to visual, auditory, and somatosensory stimuli within this near-body space, highlighting PPS boundaries' complex and flexible nature and the need for multisensory processing in spatial awareness (Geers & Coello., 2023).

However, not all objects within our peripersonal space belong to us; some may belong to others. This creates an intriguing scenario where there is both an impulse to interact with objects in our immediate space and a hesitation to handle items that belong to someone else (Constable et al., 2011, 2014; Lenglart et al., 2024). Knowing who owns an object, referred to as object ownership, is thus essential for successful interactions with both objects and individuals. For instance, being the owner of an object allows it to be processed faster and more accurately than others' objects (Ashby et al., 2012; Cunningham et al., 2008; Truong & Todd., 2017). This facilitation is tied to the self-relevance effect, of which object ownership is a specific instantiation

#### 6.2.2. Introduction

(Truong & Todd, 2017). The capacity to prioritize self-relevant information represents thus a fundamental perceptual and cognitive bias, influencing numerous aspects of human cognition (see Cunningham & Turk, 2017, for a review). Given the social environment we evolve in, selfprioritization thus optimizes cognitive resources by focusing on self-relevant cues, thereby enhancing our ability to act quickly and effectively in interpersonal contexts (Humphreys & Sui, 2016). To account for self-prioritization effects, Humphreys and Sui (2016) proposed that information relevant or referring to the self engages the self-attention network (SAN). This network integrates neural circuits responsible for processing self-related stimuli with those involved in attentional control, enhancing the processing of self-related information through the interplay of top-down and bottom-up mechanisms. According to the SAN hypothesis, the ventromedial prefrontal cortex (vmPFC) serves as a critical "self-relevance hub", integrating topdown attentional processes-primarily involving the dorsolateral prefrontal cortex (dlPFC) and the intraparietal sulcus (IPS)-with bottom-up attentional processes, which predominantly engage the posterior superior temporal sulcus (pSTS). This hypothesis, therefore, posits a neural predisposition that favours the processing of self-relevant information over information relating to others. However, the automaticity of the self-prioritization effect was recently questioned in tasks where the self-reference of stimuli was not relevant. In that case, the effect of self-prioritization was reduced (Clarkson et al., 2022) or even absent (Caughey et al., 2021; Falbén et al., 2020), suggesting that the brain may prioritize information relevant to the self, depending on contextual factors. In line with this assumption, prioritization of self-owned objects was predominantly found when processing objects in PPS, not in extrapersonal space (EPS, Lenglart et al., 2023, 2024; Patané et al., 2021). However, there remains a limited understanding of the neural mechanisms underlying the influence of contextual and social constraints on prioritization processes.

Electroencephalography (EEG), particularly through the examination of temporally sensitive event-related potentials (ERPs), is a valuable method for examining the neural dynamics of objects processing. When applied to objects' perception in space, evidence shows that the prioritization of objects situated within the PPS affect early ERPs, with, for instance, a faster and larger N1 for stimuli located in the near compared to far space (Valdés-Conroy et al., 2014). The modulation of the lateral occipital N1, an ERP associated with visual early perceptual processes (Heinze et al., 1994; Hillyard et al., 1998; Johannes et al., 1995; Mangun, 1995), aligns with the typical characterization of PPS as benefiting from prioritized processing due to its privileged role in perception and action. However, these studies did not investigate the effect of object ownership depending on location in space. Notably, the literature addressing the dynamics of neural processes related to highly self-relevant information (such as faces or impersonated visual shapes) has reported modulation in ERPs associated with early visual processing (N1 component, Liu et al., 2016; Sui et al., 2023), although such early modulation was not systematically observed (Eichenlaub et al., 2012; Miyakoshi et al., 2007). Other studies demonstrated that a range of selfrelevant (Keyes & Brady, 2010; Perrin et al., 2005; Tacikowski & Nowicka, 2010; see Knyazev, 2013 for a review) and self-owned (Miyakoshi et al., 2007; Muñoz et al., 2020) objects elicit a stronger P3 response. This evidence aligns with the broader view of P3 modulation as an indicator of how higher-order cognitive functions influence post-perceptual decision making (Kok, 2001; Nieuwenhuis et al., 2011; Verleger et al., 2005).

As object-ownership might also be influenced by the social context, it would also be interesting to analyse anterior N2 and anterior N400 ERP components, which were not considered so far as related to ownership. Indeed, previous studies have shown that a larger frontal N2 component reflects the inhibitory mechanisms involved in processing objects that need to be

averted (i.e., irrelevant or dangerous objects, Liu et al., 2023; Mustile et al., 2021; Orlandi & Proverbio, 2019), which may arise for objects perceived as not 'ours'. Likewise, enhanced anterior N400, found to reflect incongruent and socially incorrect situations (Huang et al., 2014; Luo et al., 2013), may be indicative of the detection of a socially incongruent situation where an object's expected ownership does not align with social norms (Brown & Hagoort, 1993; Huang et al., 2014; Kutas & Federmeier, 2011; Luo et al., 2013).

In this context, the present study aimed to investigate the neural temporal correlates of the interaction between object ownership and spatial location in a social virtual environment including the presence of a virtual character. Specifically, we examined how the dynamic of neural correlates of self-prioritization varies in peripersonal space (PPS) versus extrapersonal space (EPS). Consistent with the methodology employed in previous studies (Lenglart et al., 2023, 2024), participants were provided with a colored cup before being required to estimate the reachability of self-owned and other-owned paper cups presented either in PPS or in EPS, while facing the virtual character. Electroencephalography (EEG) recordings were conducted as participants performed the reachability judgment task. We hypothesized that object location in PPS versus EPS and the distinction between self- and other-objects ownership would elicit differential event-related potentials (ERPs). Specifically, we hypothesized that early perceptual ERPs, such as the N1, would differ based on objects' spatial location, with a larger amplitude and shorter latency for objects presented in PPS compared to EPS. Second, we predicted that later ERP components would be modulated by object ownership. Specifically, in agreement with self-prioritization effects, we expected the P3 amplitude to be higher for self-owned objects, although predominantly when located in PPS. Additionally, we performed an exploratory analysis of the N2 and N400 ERP

components as they might respectively be modulated by motor inhibition and incongruent context (i.e., self-owned objects in EPS or other-owned objects in PPS).

#### 6.2.3. Materials and Method

#### **Participants**

Thirty right-handed participants completed the study. The sample size of 30 participants was determined in advance using G\*Power software (version 3.1.9.7). Based on a significance level of 0.05 and a statistical power of 80%, a minimum of 24 participants was calculated to be sufficient to detect a medium effect size in a  $2\times2$  repeated-measure ANOVA (Cohen's F = 0.25), building on prior research that investigated how social and conceptual factors influence peripersonal space representation (Coello & Bonnotte, 2013; Gigliotti et al., 2021; Lenglart et al., 2023). To account for potential attrition or data loss due to noisy physiological recordings, we opted to recruit 30 participants. Two participants were excluded because of excessive noise in the EEG signal: therefore, twenty-eight participants were included in the data analysis (22 women,  $M_{age} = 21.43$ , SD = 2.78). All participants had a corrected or corrected-to-normal vision and were certified as having no history of psychiatric or neurological disease. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Participants received an information letter one week before coming to the experiment. They gave their informed consent upon their arrival at the experimental site, prior to the beginning of the experimental session. The experimental protocol was conducted in accordance with the ethical principles of the Declarations of Helsinki (World Medical Association, 2013) and was approved by the University of Lille Institutional Ethics Committee (Ref. No. 2022-634-S109).

#### Materials

#### 6.2.3. Materials and Method

The experimental tasks were created on Octave (version 7.3.0) and conducted on a 27-inch screen with a resolution of 1920 × 1080 pixels located at a distance of 60 cm from the participant, in a closed experimental room. The tasks were conducted using images of a virtual environment designed with Unity (version 2021.3.13f1) composed of a table of 150 cm long with a 3D wood texture, at the extremity of which a neutral-faced character taken from the ATHOS database (Cartaud & Coello, 2020) was seated (see Figure 20). No spatial cue biasing the perception of distance or allowing for the development of strategies by participants was available in the virtual environment.

Two real colored cups (blue or yellow) were used in order to induce object ownership. The two colored paper cups were replicated in the virtual environment and constituted the stimuli. The two cups were designed to be isoluminant in Unity, with a luminance value of 100% (HSV) and maintained a comparable contrast ratio against the table once placed in the virtual environment (yellow cup to table ratio: 1:6.36; blue cup to table ratio: 1:6.08). One cup was selected by the participant (the self-owned cup) and the other was the cup attributed to the virtual character (the other-owned cup). To notice, 56% of the participants spontaneously selected the blue cup (thus 44% of the participants selected the yellow cup).

The experimental tasks started with an initial reachability judgment task, in which the cup presented on the table was a neutral grey cup (i.e., with no ownership). The latter was presented at 29 different distances ranging from 5 to 145 cm from the proximal edge of the table, with a 5 cm inter-target distance. At the end of this task, a reachability threshold was automatically computed for each participant using the formula:

$$y = \frac{exp(\alpha + \beta x)}{1 + exp(\alpha + \beta x)}$$

were x represents the distance of the cup on the table and y represents the participant's probability of estimating the cup as "reachable". The reachability threshold obtained from the initial reachability judgment task corresponded to  $-\alpha/\beta$  and served to segment, for each participant, the table into a PPS and EPS region. The initial reachability judgment task was followed by the main task, a reachability judgment task with ownership, including self- and other-owned cups (yellow and blue) instead of the gray cup. Each of the two cups was individually presented at differently distances randomly selected along the midline of the table, either in the PPS or in the EPS. The distances corresponding to PPS were determined by subtracting 50%, 60%, or 70% of the previously computed reachability threshold, while the distances corresponding to EPS were obtained by adding 50%, 60%, or 70% to the reachability threshold (Wamain et al., 2016). To increase the complexity of the task, filler trials in which a cup was presented near the reachability threshold (at -10%, 0% and +10% of the reachability threshold) were added (10% of the trials). Each stimulus was presented until the participants provided their reachability response. For both the initial reachability judgment task and the main task, a mask consisting of a gaussian blur applied to the virtual environment with no cup on the table (see Figure 20) was presented for 1000 ms between each trial.

After the experimental session, participants were asked to answer a questionnaire composed of two questions assessing the feeling of ownership they developed for their cup ("How strongly did you feel that the cup you chose belonged to you?"). To ensure that they also acknowledged that the other mug was that of the virtual character (and not a neutral one), they were similarly asked to rate the extent to which they felt that the other mug belonged to the

#### 6.2.3. Materials and Method

confederate ("How strongly did you feel that the other cup belonged to the virtual character?"). Responses were reported on a Likert scale from 0 ("Not at all") to 7 ("Completely").

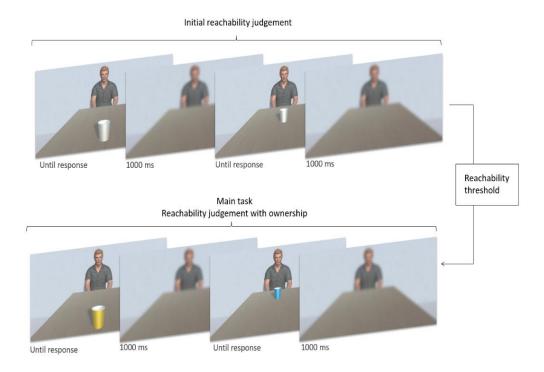


Figure 20. Illustration of the time course of the initial reachability task and of the main reachability judgment task with ownership. The blurred mask was displayed before the beginning of each trial.

#### Procedure

After arriving at the experimental site, participants selected one of two colored cups (blue or yellow) in order to induce object ownership. The participants were informed that the cup was theirs and that they could keep it and use it freely, including for drinking water after the experiment. They were also told that the other cup thus belonged to the virtual character they would see after. Both cups remained visible in the environment until the experimental tasks began to prevent

habituation effects specific to the cup selected by the participant. After this ownership induction, EEG electrodes were placed on the scalp, and participants were seated in front of a computer screen displaying the image of the virtual environment. The participants then performed successively the initial reachability judgment task (with the neutral grey cups) and the main task (with the yellow and blue cups). At the beginning of each task, participants were instructed to perform the task as fast as possible while still minimizing errors.

Participants started with the initial reachability judgment task to assess their individual reachability threshold. In this task, the grey cup was randomly displayed at different distances on the virtual table. For each trial, participants were asked to estimate if they could reach the cup with their right hand without moving their shoulders or their trunk and responded by pressing the left button of the response box with their left thumb if the cup was reachable, or by pressing the right button of the response box with their right thumb if it was not reachable (response buttons were counterbalanced across the participants). After each trial, the blurred mask was presented for 1000 ms. Participants underwent 116 trials, as the cup was presented four times at each of the 29 distances.

After the initial reachability judgment task, the experimenter asked the participants to confirm which cup was the one that they owned, and reminded them that the other one belonged to the virtual character they faced. To illustrate this ascription of ownership, a virtual scene representing the cup of the participant near themselves and the cup of the virtual character near him was displayed at the same time. In the main task, the instructions given to the participant were the same as in the initial reachability judgment task, except that they were informed that the cups would be colored and were explicitly asked to estimate the reachability of all cups from their own perspective to avoid confusion. The task consisted of seven experimental blocks. In each block,

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the two cups were presented eight times at three distances within both the PPS and EPS. To increase task complexity, 24 filler trials were incorporated, during which each cup was displayed 12 times near the reachability threshold computed for each participant. Each block comprised 120 trials (2 spaces × 3 distances × 2 colours × 8 repetitions + 24 filler trials). The entire experiment lasted approximately one hour.

#### Data acquisition

During the experiment, electroencephalographic (EEG) data were continuously recorded with a 64-channel BioSemi© ActiveTwo system (BioSemi B.V., Amsterdam) at a sampling rate of 1024 Hz on ActiView software. The electrodes were positioned following the International 10-20 system, using a cap tailored to fit the participants' head size. The electrode offsets (i.e. the voltage difference between each electrode and the CMS-DRL reference) were kept under 50 μV. Horizontal and vertical eye movements were monitored by recording electrooculographic activity using electrodes placed near each eye's canthi and below the left eye. Behavioral data were recorded using the response box located on the table near the participants and used to provide their answers with their left and right thumbs.

#### Data Processing and Analysis

Offline analysis of EEG signals was performed using BrainVision analyzer 2.1 (Brain Products GmbH, Munich, Germany). EEG signals were re-referenced to the left mastoid electrode and signal was band-pass filtered at a 1-80Hz (zero-phase shift Butterworth filter, order 2) to

remove linear trend, as required to perform optimal ICA-based artifact detection (Klug & Gramann, 2021) and effective baseline adaptation for the method of the Fractional Area Latency (see below). Blinks were removed using ICA and artifacts in the signal were manually removed. EEG signals were epoched into 1400 ms segments starting from 300 ms before and until 1100 ms after stimulus onset. The mean EEG activity within the -200 to 0 ms time window relative to stimulus onset was used as the baseline for each trial. Single-trials EEG were then baseline-corrected and averaged for each Space (Peripersonal or Extrapersonal) and Ownership status (Selfowned or Other-owned), resulting in 4 measure groups per participant.

Statistical analysis on N1, N2, P3 and N400 ERPs were conducted for all participants and all 4 measure groups. To reduce Type-I error, the clusters of electrodes and time windows used in the analysis were selected on the basis of the literature and verified following the collapsedlocalizer approach (Kappenman & Luck, 2016; Luck, 2014; Luck & Gaspelin, 2017): a grandgrand averaged waveform was formed by collapsing the data from all measure groups and all participants, and the cluster of electrodes where the amplitude of the ERP was the most pronounced was selected for the analysis (Figure 21a). On the basis of this this grand-grand average, the selected time windows were 110-220ms for the N1, 220-300ms for the N2, 290-400ms for the P3 and 370-540 ms for the N400. To measure ERPs, electrodes were averaged within regions of interest (Figure 21b): the N1 was measured at a lateral parieto-occipital cluster (P5, P6, PO3, PO4, PO7, PO8, O1,O2), the N2 and N400 at a fronto-central cluster (Fz, F1, F2, FCz, FC1, FC2), and the P3 at a parietal cluster (CPz, CP1, CP2, PZ, P1, P2). As recommended in previous studies (Kappenman & Luck, 2016; Luck, 2014), the area amplitude for the P3 and the N400 was obtained by averaging the amplitude over the time windows. Due to the narrower nature of earlier components and in order to take into account temporal variability, the mean amplitude over the

#### 6.2.3. Materials and Method

midpoint of the ERP was used for the N1 and N2. The use of the midpoint of the ERP was indeed considered as one of the most effective ways to identify peaks and latencies of ERPs (Luck & Gaspelin, 2017). The midpoint was determined through the method of the Fractional Area Latency (Luck., 2014): the time at which 50% of the cumulative amplitude of the ERP was reached was measured following the method and baseline adaptation described in Liesefeld et al. (2016), and the mean amplitude of the  $\pm$  10 ms period around this peak was selected for analysis.

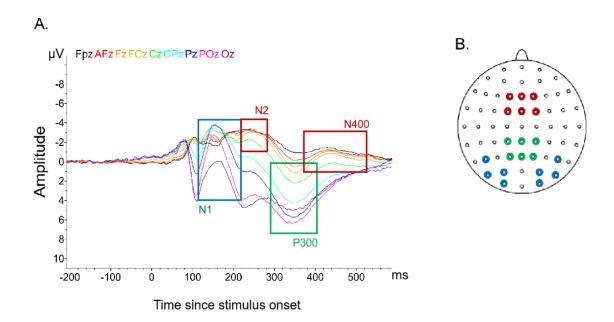


Figure 21. (A) Grand-grand average (i.e. grand average of the signal for all participants and all conditions) used for the method of the collapsed localizers. (B) Clusters of electrodes used for the analyses. The red electrodes constitute the fronto-central cluster, the green electrodes the parietal-central cluster, and the blue electrodes the lateral parieto-occipital cluster.

Electrophysiological and behavioral data were analysed with R version 4.4.0. Linear mixed-models were used to analyse data as a function of Space (Peripersonal, Extrapersonal) and Ownership status (Self-owned, Other-owned) as fixed effects using the packages *lme4* (v1.1–35.3; Bates et al., 2015) and *lmerTest* (v3.1-3; Kuznetsova et al., 2017). The model also took into account

inter-individual differences by systematically including participants as a random effect. Given the close temporal and spatial relationship between the N1 and its preceding potential, the P1, we additionally included the P1 amplitude (measured at 80-140 ms at parieto-occipital electrodes) as a random effect in the N1 analyses to account for possible P1 amplitude effects on the N1. The maximal random effect structure supported by the data and the model was chosen when possible. When the model did not converge or over-fitted, theoretical consideration were taken into account to reduce the random effect structure. For significant effects, effect sizes were determined using Westfall's d, an alternative to Cohen's d for linear mixed models, computed with the eff\_size function of the *emmeans* package (v1.10.2; Lenth, 2024). Significant interactions were further investigated via paired-samples *t*-test using the package *emmeans*, and all comparisons were corrected with the multivariate *t* correction, as suggested by Lenth (2024): this correction uses the multivariate *t*-distribution, via Monte Carlo simulations, to estimate critical values or probabilities for the maximum of *k* estimates while accounting for their dependency and controlling the family-wise error rate. Normality was assessed by visual inspection of the residuals.

#### 6.2.4. Results

In the pre-experiment reachability judgment, participants estimated, on average, that they could reach the cup located in the virtual environment at distances of up to  $64 \pm 14$  cm. In addition, participants were requested, after the experiment, to rate the feeling of ownership that they had felt toward their cup and the one that they had felt between the confederate and his cup on a scale from 0 to 7 (0 being "no feeling of ownership at all" and 7 being "a very strong feeling of ownership"). On average, participants reported a fairly high sense of ownership toward their cup (M = 4.45, SD

= 1.62) and a slightly weaker sense of ownership between the confederate and his cup (M = 3.35, SD = 1.76).

#### Behavioral data

Overall, participants made few errors, with an average of 14.4 errors during the task (Mdn = 10). Of these, 54% of errors occurred in the PPS, with an interquartile range (IQR) of 32% to 80%. In the PPS, the majority of errors occurred when the cup was other-owned (Mdn = 94%, IQR = [66% - 100%]) while, in the EPS, the majority of errors occurred when the cup was self-owned (Mdn = 75%, IQR = [48% - 100%]).

The repeated-measures linear mixed model conducted on reaction time (RT) revealed a main effect of Space ( $\beta = -0.05$ , t = -7.09, SE = 0.01, p < .001, Westfall's d = 2.52): the RT was faster in the PPS (M = 0.47s, SD = 0.10) compared to the EPS (M = 0.52s, SD = 0.11, Figure 22). In addition, the interaction between Space and Ownership was significant ( $\beta = -0.03$ , t = -5.47, SE = 0.01, p < .001, Westfall's d = 0.81). Participants responded significantly faster when their own cup was displayed within the peripersonal space (PPS; M = 0.46 s, SD = 0.97) compared to the confederate's cup (M = 0.47 s, SD = 0.10;  $\beta$  = 0.02, t = 3.90, p < .001,  $p_{mvt}$  = .001, Westfall's d = 1.04). Conversely, participants displayed lower RT to respond when the confederate's cup was displayed in the extrapersonal space (EPS; M = 0.51 s, SD = 0.11) compared to their own cup in the same location (M = 0.53 s, SD = 0.12;  $\beta$  = 0.02, t = 3.85, p < .001,  $p_{mvt}$  = .001, Westfall's d = 1.03). In addition, participants were faster to react when their own cup was located in the PPS (M = 0.51s, SD = 0.11) compared to in the EPS (M = 0.53s, SD = 0.12,  $\beta = 0.07$ , t = 8.65, p < .001,  $p_{\text{myt}} < .001$ , Westfall's d = 4.26), and when the other's cup was located in the EPS (M = 0.51s, SD = 0.11) compared to in the PPS (M = 0.53s, SD = 0.12,  $\beta = 0.03$ , t = 4.45, p < .001,  $p_{\text{myt}} < .001$ , Westfall's d = 2.19). Lastly, no main effect of Ownership was observed ( $\beta < 0.01$ , t = -0.03, SE < 0.01

0.01, p = .976). Indeed, participants were, on average, as fast to answer when their cup was displayed (M = 0.49s, SD = 0.11) compared to that of the confederate (M = 0.49s, SD = 0.10), regardless of location in space.

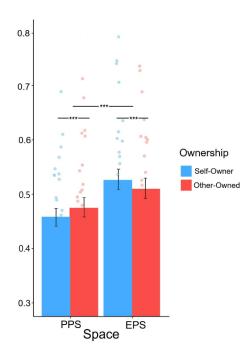


Figure 22. Mean response time as a function of Space and Ownership. Asterisks indicate statistical significance.

#### EEG data

#### Parieto-occipital N1

The analysis of the mean peak amplitude of the N1 revealed that there was no main effect of Space ( $\beta$  = 0.02, t = 0.12, SE = 0.22, p = .908), Ownership ( $\beta$  = -0.05, t = -0.35, SE = 0.15, p = .726) or interaction between Space and Ownership ( $\beta$  = -0.03, t = -1.00, SE = 0.30, p = .924) for the mean peak amplitude of the N1. By contrast, a significant main effect of Space ( $\beta$  = -6.66, t = -5.44, SE = 1.22, p < .001, Westfall's d = 2.76, Figure 23) was observed for the latencies of the N1.

Specifically, N1 latency was found to be shorter when the cup appeared in PPS (M = 156.92ms, SD = 13.68) as opposed to when it appeared in EPS (M = 167.63ms, SD = 9.95). Again, no effect of Ownership ( $\beta = -0.93$ , t = -0.90, SE = 1.03, p = .370) and no interaction between Ownership and Space was found ( $\beta = 0.54$ , t = 0.37, SE = 0.30, p = .715).

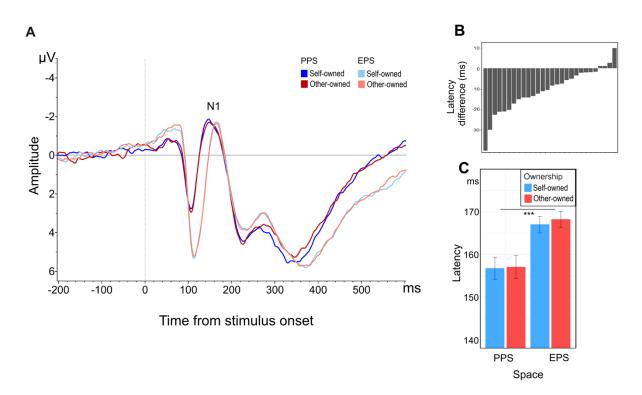


Figure 23. (A) Grand-average ERP at the lateral parietal-occipital cluster. (B) Scalp topography of the N1 over the time window of interest. (C) Individual PPS - EPS differences in the N1 latency. (D) N1 latency as a function of Space and Ownership. Asterisks indicate statistical significance.

#### Centro-parietal P3

The P3 amplitude analysis yielded a significant Ownership × Space interaction ( $\beta$  = 71.91, t = 3.044, SE = 23.63, p = .005, Westfall's d = 1.30, Figure 24). Paired-sample t-tests revealed that the area amplitude of the P3 was larger when the cup presented in the PPS was self-owned (M = 453.05 $\mu$ V, SD = 244.11), compared to other-owned (M = 391.87 $\mu$ V, SD = 258.50, t = -3.43, p =

.001,  $p_{mvt} = .004$ , Westfall's d = 0.98), whereas no significant differences were observed for the remaining contrasts (all p > 650). No main effect of Space ( $\beta = 5.55$ , t = 0.15, SE = 36.22, p = .879) and no main effect of Ownership ( $\beta = 25.22$ , t = 1.89, SE = 13.33, p = .069) was observed.

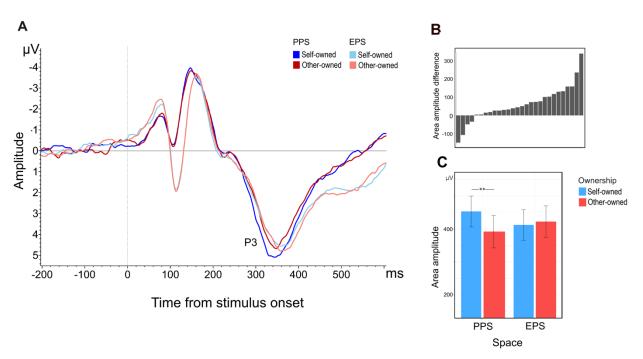


Figure 24. Grand-average ERP at the parietal cluster. (B) Scalp topography of the P300 over the time window of interest. (C) Individual Self - Other differences in PPS in the P300 amplitude. (D) P300 amplitude as a function of Space and Ownership. Asterisks indicate statistical significance.

#### Frontal N2

The analysis conducted on the mean peak amplitude of the N2 revealed a main effect of Space ( $\beta$  = -0.91, t = -3.01, SE = 0.30, p = .003, Westfall's d = 1.85, Figure 25). In particular, the amplitude of the N2 was larger when a cup appeared in the PPS (M = -3.83 $\mu$ V, SD = 2.52) compared to when it appeared in the EPS (M = -2.89 $\mu$ V, SD = 2.17). There was, however, no significant main effect of Ownership ( $\beta$  = -0.08, t = -0.27, SE = 0.30, p = .788) and no effect of interaction between Ownership and Space ( $\beta$  = -0.05, t = -0.11, SE = 0.43, p = .912).

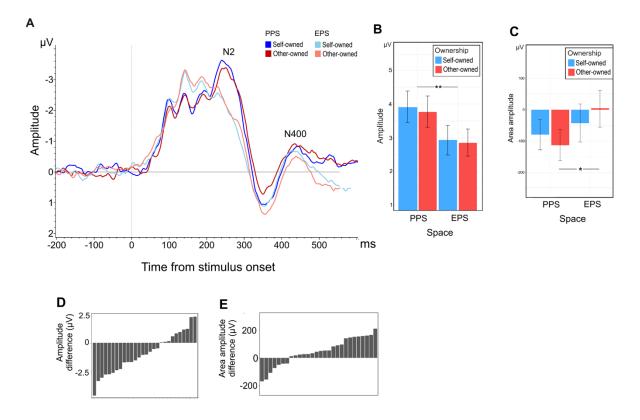


Figure 25. Grand-average ERP at the fronto-central cluster. (B) N2 amplitude as a function of Space and Ownership. Asterisks indicate statistical significance. (C) N400 amplitude as a function of Space and Ownership. (D) Individual PPS - EPS differences in the N2 amplitude. (E) Individual PPS - EPS differences in the N400 amplitude.

#### N400

A significant effect of Space on the N400 peak amplitude ( $\beta$  = -115.70, t = -2.56, SE = 45.20, p = .015, Westfall's d = 1.22) was observed. Specifically, the amplitude was larger when cups were located in the PPS (M=-95.45 $\mu$ V, SD = 272.23) compared to in the EPS (M=-19.12 $\mu$ V, SD = 329.41). Additionally, a significant effect of Ownership ( $\beta$  = -45.48, t = -2.13, SE = 21.34, p = .037, Westfall's d = 0.79) was found, with self-owned cups eliciting a larger amplitude (M = -60.34 $\mu$ V, SD = 302.50) compared to other-owned cups (M=-54.23 $\mu$ V, SD = 306.70). A significant

Ownership × Space interaction was also observed ( $\beta = 78.73$ , t = 2.67, SE = 29.53, p = .013, Westfall's d = 0.58, Figure 25). Follow-up paired-sample t-tests revealed that the amplitude of the N400 was quasi-significantly larger when the other-owned cup was presented in the PPS ( $M = -112.08 \mu V$ , SD = 327.95) compared to the EPS (M = 3.62, SD = 277.71, t = -2.56, p = .015,  $p_{mvt} = .051$ , Westfall's d = -1.48). No significant differences were observed in the remaining comparisons (all  $p_{mvt} > 0.12$ ).

#### 6.2.5. Discussion

We employed electroencephalography (EEG) to investigate the neural correlates of cognitive processes underlying the processing of self- and other-owned objects as a function of their position in the peripersonal (PPS) or extrapersonal (EPS) space. Our results revealed significant effects of space on early and late ERP components, as well as complex interactions between spatial context and ownership on later ERP components. These results provide new insights into the understanding of how the brain dynamically integrates spatial and social information for object-directed motor behaviour.

Concerning behavioral performances, the present study provides congruent outcomes concerning previous studies that have investigated the relationship between space and ownership in object processing (Lenglart et al., 2023, 2024). In particular, we observed that the time required to judge reachability was faster for self-owned objects compared to other-owned objects, in particular in the PPS. Indeed, reachability judgments for self-owned cups compared to other-owned cups were shorter in the PPS, and longer in the EPS. In addition, the advantage of self-owned objects compared to other-owned objects observed in the PPS inverted in the EPS. Overall, the data suggest a facilitation of object processing when located in the PPS (Blini et al., 2018;

Costantini et al., 2010; Spence et al., 2004), which is enhanced with self-owned objects (Constable et al., 2011; Lenglart et al., 2023, 2024).

In line with the behavioral data, ERP analysis revealed that the N1 component, associated with perceptual processing and attentional enhancement, peaked earlier in the reachability judgment task when the cup was located in the PPS compared to when the cup was located in the EPS. These results are in agreement with the extensive literature proposing that the processing of information in PPS is prioritized through sensory enhancement, consistently with its special role in facilitating rapid detection of stimuli near the body (Brozzoli et al., 2011; Lenglart et al., 2024; Serino et al., 2009). These findings provide additional neurophysiological evidence that PPS is a specialized space enhancing perceptual processing in preparation for potential action (Graziano & Cooke, 2006; Serino, 2019) and that this enhancement holds in a non-immersive virtual environment.

However, no effect of ownership on N1 amplitude was observed, which seems to indicate that ownership does not influence such early processes. This finding challenges the traditional view of self-relevance as a common mechanism capable of consistently capturing attention in a bottom-up manner (Humphreys & Sui, 2016; Sui & Rotshtein, 2019). An interpretation for the absence of ownership-related effects on the N1 could be that the self-relevance of objects used for action does not elicit responses as strong as more familiar forms of self-relevant stimuli (such as one's own name for instance, Cunningham & Turk, 2017; Schäfer & Frings, 2019), which have been shown to influence early processes (Nijhof et al., 2018; Sui et al., 2012).

By contrast, we observed that the amplitude of the P3 was larger for self-owned cups, compared to other-owned cups, but only when they were located in the PPS. The P3 component is

usually considered as a neural marker of the mediation between the perceptual analysis and the response initiation during decision-making (Nieuwenhuis et al., 2011; Verleger et al., 2005). Its amplitude is thus larger for personally or contextually relevant information (Baines et al., 2011; Franken et al., 2011; Polich, 2007), reflecting an increased allocation of cognitive resources (Hoffman et al., 1985; Isreal et al., 1980; Strayer & Kramer, 1990). Thus, self-ownership appears to facilitate decision-making by optimizing the processing of perceptual inputs, which in our study seems limited to PPS. This suggests that motivationally significant information (i.e. information relevant to the current task or showing utility for oneself, Nieuwenhuis et al., 2011) is prioritized at a post-perceptual stage.

We further observed a larger frontal N2 amplitude for objects located in the PPS compared to those located in the EPS, with no effect of object ownership. Classically, this ERP is associated with the inhibition of the motor system (Falkenstein et al., 1999; Liu et al., 2023; Proverbio et al., 2011). However, other authors hypothesized that the N2 can also reflect the strength of the coupling between perception and action: for instance, the N2 is larger when perceiving tools instead of natural objects (Proverbio et al., 2011, 2013; Proverbio, 2012). Interestingly, it seems that this modulation is only observed in studies where the manual configuration of the action afforded by a particular object and the modality of the response are different (Mustile et al., 2021; Proverbio et al., 2011, 2013; Proverbio, 2012). In our task, the motor configuration required to reach the cup in the PPS did not correspond to the motor configuration required for the task's response, requiring a reconfiguration of the initial motor plan for the participant. We thus propose that the N2 was rather elicited by the inhibition of the unexecuted action (or inhibition-related conflict). In other words, it was associated with the suppression of a latent motor plan.

Finally, we observed that N400 amplitude was larger when the self-owned cup was placed in EPS, closer to the virtual character. Incongruent and socially incorrect situations are, in EEG studies, reflected through the N400 (Huang et al., 2014; Luo et al., 2013), an ERP historically associated with semantic incongruence (Brown & Hagoort, 1993; Kutas & Federmeier, 2011) and observed at anterior sites during the processing of objects and action-related information (Amoruso et al., 2013; Van Elk et al., 2010; Võ & Wolfe, 2013). In the context of object-ownership, an enhanced anterior N400 may thus reflect the processing of a socially incongruent situation, which could arise when a self-owned object is located near a stranger (here, the virtual character).

Although the present findings offer new insights into the influence of ownership on object processing for action, other influential factors may require consideration. For instance, objects in the PPS were predominantly located lower in the visual field compared to those in the EPS. Given its proximity to the body, PPS is inherently linked to lower visual field perception closely related to the dorsal visual neural pathway, functionally specialized in action-related processing (Previc, 1990). To minimize potential confounds, we designed the virtual table to occupy only the lower half of the screen, and did not impose any constraints on gaze direction before the objects were presented at different locations. Nevertheless, the extent to which the observed effects may be dependent on the position of objects in the visual field remains an open question. Additionally, other conceptual properties of objects, such as affective meaning or prior interaction history, may also modulate the strength of ownership (Morewedge, 2021) and thus the processing of near objects for action. Investigating these influences represents promising avenues for future research and could provide complementary insights into the cognitive and neural mechanisms underlying object processing during object-directed action in more ecological contexts.

In sum, our findings highlight the distinct neural dynamics underlying the processing of spatial and ownership-related information in a task requiring estimating objects reachability. Prioritization of the PPS was observed during the early stage of object processing, as evidenced by the modulation of the latency of the N1 component. This prioritization aligns with the neurophysiological evidence supporting the unique and adaptive status of PPS in ensuring rapid detection and processing of stimuli, in line with its role in goal-directed behaviour and protection of the body. In contrast, ownership effects emerged at later stages of object processing, as evidenced by the larger P3 amplitude for self-owned objects, suggesting that self-relevant information becomes motivationally significant during post-perceptual stages, although predominantly in the PPS. This finding supports the view that self-relevance operates in a contextdependent manner, selectively enhancing information based on task-specific utility rather than universally prioritizing all self-associated stimuli. Unlike tasks integrating highly familiar aspects of self-relevance or identity—where the Self-Attention Network (SAN) has been shown to facilitate early attentional capture (e.g., Sui et al., 2012)— our results indicate a more selective allocation of cognitive resources, congruent with an action-oriented framework emphasizing goaldirected processing. Overall, our findings highlight the adaptive and flexible nature of selfrelevance attribution, dynamically interacting with spatial information to optimize goal-directed behaviour in the environment. Complementary studies would however be required, in particular to confirm the present findings in different contexts and investigate the neural network supporting those findings using brain imaging techniques.

#### **Author contribution**

Lucie Lenglart: Conceptualization; methodology; software; investigation; data curation; formal analysis; project administration; visualization; writing – original draft. Clémence Roger: Conceptualization; methodology; supervision; visualization; writing – original draft. Adriana Sampaio: Supervision; writing – original draft. Yann Coello: Conceptualization; funding acquisition; methodology; project administration; supervision; visualization; writing – original draft.

#### **Conflict of interest statement**

The authors declare no conflict of interest.

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#### 7.1. Foreword

### 7. THE CONTEXTUAL SELF: OBJECT OWNERSHIP MODULATES NEURAL ENCODING ACROSS PERIPERSONAL AND EXTRAPERSONAL SPACES

#### 7.1. Foreword

The findings presented thus far demonstrated that object ownership and spatial location interact during object processing for efficient action, particularly through motor-related mechanisms. In Chapter 6, we observed that this interaction followed a temporal sequence: spatial information, notably the presence of an object in the PPS, biased processing at an early perceptual stage, whereas ownership information was integrated later. Self-ownership was indeed prioritized at a post-perceptual, possibly decisional stage, while other-ownership was integrated during contextual evaluation.

However, the neural correlates of this interaction remain to be clarified. Previous research has associated the processing of information in the PPS with activity in a fronto-parietal network including the premotor cortex and posterior parietal areas, particularly the intraparietal sulcus. In contrast, the processing of object ownership and self-relevance has been linked to activations in medial prefrontal regions (mPFC) with functional distinctions between its dorsal and ventral subdivisions, the latter being often proposed as a central node for self-referential processing.

The following fMRI study aimed to investigate how these distinct but potentially interacting networks contribute to the processing of self- versus other-owned objects located in near and far space. We hypothesized that if the prioritization of self-owned objects in the PPS reflects the integration of spatial and social-conceptual information to prepare possible action, then we should observe a modulation of the fronto-parietal PPS network. A second aim was to understand if the involvement of the ventral mPFC in the self-related processing (and, to a lesser extent, of the dorsal mPFC for other-related processing) was obligatory and consistent across context, or whether it is sensitive to contextual relevance.

#### 7.2. MAIN STUDY

# The Contextual Self: Object ownership modulates neural encoding across peripersonal and extrapersonal spaces

Lenglart, L.<sup>1,2,3</sup>, Coello, Y.<sup>1,2</sup>, Sampaio, A.<sup>3</sup>

- 1. Univ. Lille, CNRS, UMR 9193 SCALab Sciences Cognitives et Sciences Affectives, 59000 Lille, France
- 2. Univ. Lille, CNRS, FR 2052 SCV Sciences et Cultures du Visuel, 59200 Tourcoing, France
- 3. Psychological Neuroscience Lab, Psychology Research Centre (CIPsi), School of Psychology, University of Minho, Braga, Portugal

#### 7.2.1. Abstract

A crucial aspect of interacting with objects in our environment lies in determining whether they are located within peripersonal space (PPS) - where immediate action is possible- or extrapersonal space (EPS), where objects are out of reach. Importantly, social context often prompts additional consideration of object ownership, which may interfere with spatial localization. Although previous research has demonstrated that both spatial and social contexts influence object processing, the neural networks subtending their interaction remain largely unexplored. To address this issue, the present fMRI study investigated the neural correlates of object ownership as a function of spatial location (PPS vs EPS). While facing a virtual character, 22 participants judged the reachability of self-owned or other-owned objects placed at varying distances. Results showed that objects located in PPS activated parietal regions implicated in the sensorimotor coding of near-space stimuli, with enhanced parietal responses observed for selfowned objects, particularly in the right hemisphere. Conversely, objects in EPS engaged prefrontal regions, especially when they were self-owned. Multivariate analyses further revealed that both the ventromedial prefrontal cortex (vmPFC) and dorsomedial prefrontal cortex (dmPFC) reliably distinguished self-owned objects, with the vmPFC selectively encoding self-ownership in PPS. These findings highlight how spatial and social dimensions jointly shape object representations in the brain, with self-relevance modulating action-related processing even in tasks focusing on spatial processing.

#### 7.2.2. Introduction

Spatial perception is inherently non-uniform. Rather than representing space as homogeneous and continuous, the brain constructs nested spatial representations, each serving distinct functional purposes. Among these, peripersonal space (PPS) refers to the immediate space surrounding the body, which is uniquely suited for guiding actions by integrating multisensory inputs in a self-centred frame of reference (Brozzoli et al., 2011; Serino, 2019). This space is distinguished from the extrapersonal space (EPS), which lies beyond the boundaries of immediate action (Serino, 2019). Importantly, PPS is not defined by fixed metric distances but by its behavioral relevance for action (Bufacchi & Iannetti, 2018). Accordingly, PPS is not a static construct but a flexible and context-sensitive representation that adapts to changing bodily and environmental constraints. For example, the boundaries of PPS expand following tool use, as the body schema incorporates the tool as an extension of the limb wielding it (Cardinali et al., 2009; Farnè & Làdavas, 2000; Iriki et al., 1996), or contract when bodily movements are restricted (Canzoneri et al., 2013; Coello et al., 2012). This plasticity allows the brain to continuously recalibrate spatial representations, thereby supporting efficient motor responses and optimizing interactions with the environment (Coello & Cartaud, 2021; Bufacchi & Iannetti, 2018).

Neurophysiological studies have established that PPS representation relies on a distributed fronto-parietal network specialized for multisensory integration and action preparation. In this respect, seminal work in non-human primates identified bimodal neurons in the ventral premotor cortex (areas F4 and F5) and in the intraparietal sulcus (areas VIP and AIP) that respond to both tactile inputs and visual or auditory stimuli presented near the body (Graziano & Gross, 1993; Fogassi et al., 1996; Rizzolatti et al., 1981; Cléry et al., 2015). In humans, convergent evidence from neuroimaging and lesion studies revealed a functionally homologous network comprising the

inferior parietal lobule (IPL), intraparietal sulcus (IPS), and the dorsal and ventral premotor cortex (PMC), selectively activated during near-space processing (Brozzoli et al., 2012; Grivaz et al., 2017; Sereno & Huang, 2006). Critically, this core PPS network does not operate in isolation but functions as part of a flexible, context-sensitive system: its recruitment is modulated via coordinated connections with other neural systems, depending on task demands, body posture, and environmental context (Basile et al., 2024).

Over the past years, PPS has also been conceptualized as a dynamic interface for social interaction. Behavioral studies have shown that during cooperative tasks, individuals adapt their PPS representation to include their partners' space, thereby facilitating coordinated action (Gigliotti et al., 2021; Teneggi et al., 2013). This remapping is supported by the construction of a representation of others' PPS, allowing for anticipated motor adjustments (Cardellicchio et al., 2013; Ruggiero et al., 2021). Neuroimaging evidence indicated that fronto-parietal regions involved in PPS representation -including the premotor and parietal cortices- exhibited activity patterns mirroring self-related processing when others are present (Brozzoli et al., 2013; Schaefer et al., 2012; Rizzolatti & Rozzi, 2018). These findings challenged strictly self-centred models of PPS, demonstrating that PPS representation also incorporates interpersonal information to support action coordination and social interaction (Coello & Cartaud, 2021).

A key dimension through which social context influences spatial representations is the attribution of object ownership. When an object is within our reach, implicit social norms can constrain our interaction with it, as objects within our PPS may belong to us or to others, depending on the context. This creates a situation where individuals simultaneous feel the urge to engage with objects in their immediate space, while also experiencing a reluctance to interact with items that belong to others (Constable et al., 2011, 2014; Lenglart et al., 2024; 2025), due to the widely

#### 7.2.2. Introduction

accepted norm that we do not spontaneously engage with other's belongings without explicit permission. Critically, individuals are motivated to maximize personal benefits while simultaneously minimizing social risks (Fujii et al., 2009). Thus, recognizing the ownership of objects in our environment is crucial for selecting and guiding appropriate interactions with both the objects and the individuals involved (Constable et al., 2014; Lenglart et al., 2025).

Beyond its role in social organization, object ownership also influences the idiosyncratic relevance of objects. When an item is perceived as belonging to oneself, it typically attains privileged status in cognitive processing. This "self-relevance effect" includes a range of advantages, such as enhanced attentional focus and improved memory encoding through preferential processing (see Cunningham & Turk, 2017, for a review). Neuroimaging studies have consistently linked this self-prioritization to changes in the activation of cortical midline structures, particularly the ventromedial (vmPFC) and dorsomedial (dmPFC) prefrontal cortices, which are recognized as key regions supporting self-referential cognitive functions (Kelley et al., 2002; Murphy et al., 2019; Sui & Gu, 2017; Tacikowski et al., 2011). Importantly, the implication of these neural regions extends from abstract self-referential information to self-owned objects. For instance, Turk et al. (2011) showed that the activity of the vmPFC and dmPFC was selectively modulated by object ownership, with the dmPFC being specifically engaged in the processing of self-owned objects. Similarly, Kim & Johnson (2012) proposed that the preferential activation of the mPFC provides evidence for the incorporation of self-owned objects into an "extended self", referring to the integration of stimuli into one's own representation of the self (Belk, 1988; Beggan, 1992). Interestingly, these regions are also involved in the broader processing of socially relevant information (Tso et al., 2018), suggesting that ownership may serve as a bridge between selfrelated and socially contextualized cognition.

However, the extent to which this self-prioritization reflects automatic processing or varies according to context remains a topic of ongoing debate (Golubickis & Macrae, 2023; Falbén et al., 2019). Recent studies, for instance, have challenged the assumption that self-relevant stimuli are invariably prioritized: when task demands do not explicitly involve self-referential processing, self-prioritization is often significantly attenuated (Clarkson et al., 2022) or even absent (Caughey et al., 2021; Falbén et al., 2020). Consistent with this interpretation, enhanced processing of selfowned objects has been observed specifically when those objects are located within PPS, rather than EPS (Lenglart et al., 2024, 2025; Patané et al., 2021). However, the neurocognitive mechanisms through which contextual factors modulate the prioritization of self-relevant objects remain poorly understood. To address this gap, the present study investigated how object ownership (self- vs. other-owned) and spatial representation (PPS vs. EPS) interact at the neural level. Using functional magnetic resonance imaging (fMRI), we investigated the involvement of the fronto-parietal network, known for its role in PPS processing, alongside brain regions typically associated with self-referential cognition. To determine whether self- and other-owned objects recruited distinct brain networks depending on their spatial location (PPS vs. EPS), participants performed a reachability judgment task adapted from previous protocols (Lenglart et al., 2024, 2025). During fMRI scanning, they estimated the reachability of cups attributed either to themselves or to another person. This design enabled us to examine (I) whether reachability judgements for self- and other-owned objects recruited similar or distinct neural networks depending on spatial context, (II) whether ownership modulated activity within the core frontoparietal PPS network, and (III), whether activation patterns within the medial prefrontal cortex distinguished between self- and other-owned objects as a function of their spatial location.

#### 7.2.3. Results

#### 7.2.3. *Results*

# Whole-brain analysis

activations in the parietal cortex. In the left hemisphere, significant clusters emerged in the superior and inferior parietal lobules (SPL and IPL; peak MNI coordinates: -26, -53, 45; see Table 1 and Figure 26a). In the right hemisphere, robust activations were observed in the SPL, IPL, and precentral gyrus (MNI: 49, -44, 54), partly corresponding to the anterior part of the intraparietal sulcus (aIPS), with an additional cluster extending to the precuneus and cuneus (MNI: 19, -68, 45). The reverse contrast (EPS > PPS) revealed widespread frontal activations. These included a cluster encompassing the left superior and medial frontal gyri (MNI: -17, 62, 15; see Table 1 and Figure 26b), as well as bilateral activation in medial orbitofrontal regions, including the frontal medial orbital and superior medial cortices.

The contrast examining the main effect of spatial location (PPS > EPS) revealed bilateral

No significant activation was observed for the main effect of ownership, as tested by the contrasts Self > Other and Other > Self, at the whole-brain level.

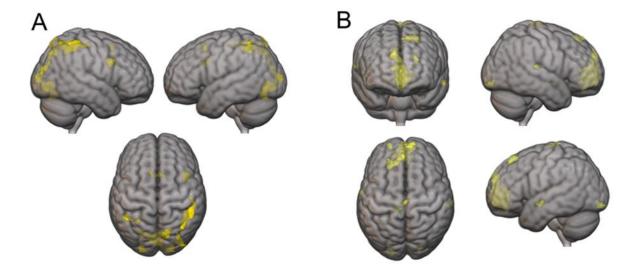


Figure 26. Brain areas more active for cups located in (A) PPS vs. EPS and (B) EPS vs. PPS, surviving at a statistical threshold of  $p_{uncorrected} < 0.001$  at the voxel level and  $p_{FDR} < 0.05$  corrected at the cluster level.

To assess how ownership and spatial location jointly modulate neural activity, we conducted a whole-brain analysis of the interaction between the four conditions. This analysis revealed two significant clusters in the frontal cortex for the contrast *Self* > *Other* in PPS compared to EPS (MNI: -23, 59, 6 and -20, 47, 45; see Table 2). These results suggest that frontal regions are sensitive to the congruency or contextual alignment between ownership and spatial proximity.

To better identify brain regions involved in processing objects in near versus far space for each ownership condition, we separately analysed the contrasts comparing PPS to EPS and EPS to PPS for self-owned and other-owned objects. For self-owned objects, the contrast *PPS* > *EPS* revealed a large right-lateralized parietal cluster extending along the anterior-posterior axis of the intraparietal sulcus (IPS), encompassing the IPL, SPL, supramarginal gyrus, and precentral gyrus (MNI: 55, -32, 57; Table 3 and Figure 27). Additional clusters were found in the right inferior frontal gyrus (rIFG; opercular and triangular parts; MNI: 59, 10, 21) and anterior precentral gyrus

(MNI: 55, 16, 12). Bilateral occipital activations were observed in the calcarine sulcus and superior occipital gyrus, with further involvement of the right cuneus and left lingual gyrus.

For other-owned objects, the *PPS* > *EPS* contrast revealed right-lateralized activations in the IPL, SPL, and supramarginal gyrus (MNI: 46, -44, 51; see Table 3 and Figure 27), though the cluster was smaller than that observed for self-owned objects. Occipital activation patterns resembled those seen in the self-owned condition, with bilateral calcarine activation, and additional clusters in the left lingual and middle occipital gyri, and right cuneus and superior occipital gyrus.

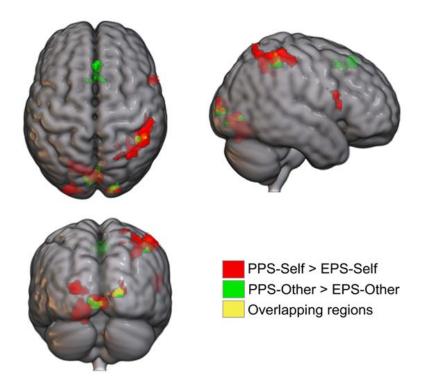


Figure 27. Brain areas more active for cups located in PPS vs. EPS for self-owned objects (red) and other-owned objects (green), surviving at a statistical threshold of  $p_{uncorrected}$  <0.001 at the voxel level and  $p_{FDR}$ <0.05 corrected at the cluster level.

The *EPS* > *PPS* contrast for self-owned objects revealed a large frontal cluster involving the left superior and medial frontal gyri, encompassing regions of the vmPFC, dmPFC, and dorsal anterior cingulate cortex (dACC; MNI: -17, 62, 15; see Table 3 and Figure 28). Additional activations were observed in the right posterior superior temporal sulcus (pSTS), right SMA, bilateral midcingulate cortex, left paracentral lobule, and left postcentral gyrus. Posterior activations included the precuneus and left inferior occipital and lingual gyri.

For other-owned objects, *EPS* > *PPS* yielded a smaller but overlapping cluster in frontal regions. This included the left superior and medial frontal gyri, orbital gyrus, and pregenual anterior cingulate cortex, extending into the superior vmPFC and ventral ACC (MNI: -5, 59, 0; see Table 3 and Figure 28).

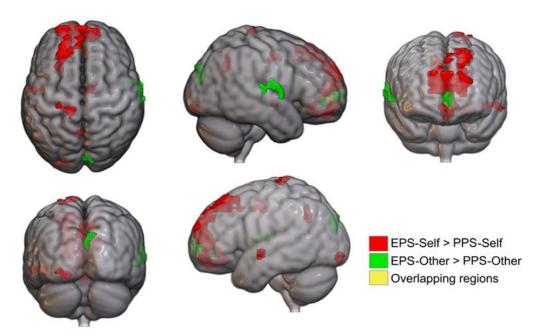


Figure 28. Brain areas more active for cups located in EPS vs. PPS for (A) self-owned objects and (B) other-owned objects, surviving at a statistical threshold of  $p_{uncorrected} < 0.001$  at the voxel level and  $p_{FDR} < 0.05$  corrected at the cluster level.

#### ROI analysis

When analyses were constrained to the fronto-parietal core PPS network, the contrast *Self* > *Other* in PPS revealed significant bilateral parietal activations. On the right hemisphere, activations were found in the IPL, SPL, and precentral gyrus (MNI: 52, -35, 57; see Table 4 and Figure 29a), while on the left hemisphere, activation encompassed the IPL, supramarginal gyrus, and postcentral gyrus (MNI: -57, -26, 45). No significant activations were observed for the reverse contrast (*Other* > *Self*) within PPS.

In the EPS condition, the contrast *Self* > *Other* did not reveal any significant clusters of activation. In contrast, the reverse contrast *Other* > *Self* identified a significant right-lateralized cluster encompassing the angular gyrus and the supramarginal gyrus (MNI: 37, –53, 45; see Table 4 and Figure 29b).

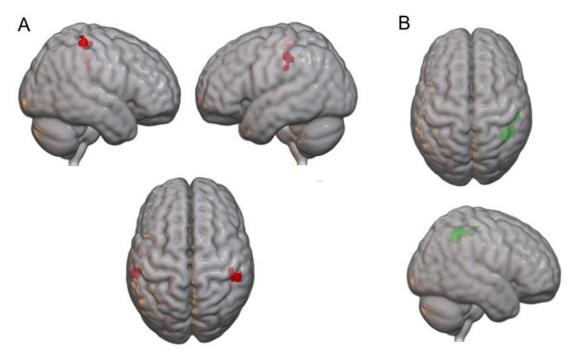


Figure 29. Brain areas more active for (A) self- vs. other-owned cups in PPS and (B) other vs. self-owned cups in EPS, surviving at a statistical threshold of  $p_{uncorrected} < 0.001$  at the voxel level and  $p_{FDR} < 0.05$  corrected at the cluster level.

# Multivariate ROI-based analysis

Multivariate pattern analysis (MVPA) revealed that activation patterns in the vmPFC carried significant information distinguishing self-owned objects presented in PPS, with classification accuracy significantly above chance (59.09%; puncorrected .001,  $p_{Bonferroni} = 0.004$ ). None of the other conditions, including self- and other-owned objects in EPS and other-owned objects in PPS, was classified above-chance in the vmPFC (all  $p_{uncorrected} > .15$ ). Notably, in EPS, classification patterns for self- and other-owned objects were descriptively similar, suggesting that classification in this context was likely driven by spatial rather than ownership-related features. This pattern may reflect the encoding of general social or contextual salience rather than self-specific processing.

In the dmPFC, classification accuracy for self-owned objects in PPS was also significantly above chance (classification accuracy = 50%,  $p_{uncorrected}$  =.01,  $p_{Bonferroni}$  = .04). A trend toward above-chance classification was observed for self-owned objects in EPS as well, though this effect did not survive correction for multiple comparisons (classification accuracy = 50%,  $p_{uncorrected}$ =.02,  $p_{Bonferroni}$  = .08). Classification performance for all other conditions in the dmPFC remained at chance level (all  $p_{uncorrected}$  >.14).

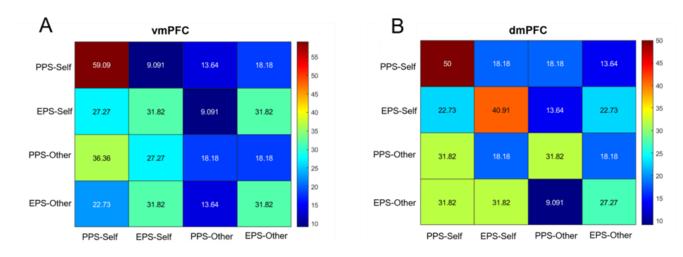


Figure 30. Confusion matrix of the multivariate pattern classification accuracy for the four experimental conditions in (a) the ventromedial prefrontal cortex and (b) the dorsomedial prefrontal cortex. Each row corresponds to the true experimental condition, and each column indicates the proportion of instances classified as each of the four possible conditions. Values represent the percentage of test instances assigned to each category, averaged across folds. Chance level is at 25%.

# 7.2.4. Discussion

The present study investigated the neural mechanisms underlying reachability judgments within peripersonal space (PPS) and extrapersonal space (EPS), focusing on how object ownership modulates spatial encoding across these domains. Our findings reveal that spatial processing in PPS and EPS engages distinct neural networks, aligning with prior research supporting a functional dissociation in the neural coding of near and far space. Crucially, this spatial encoding is not uniform across all stimuli: object ownership introduced socially grounded conceptual meaning that differentially influenced neural processing depending on the spatial context.

# **Neural representation of PPS and EPS**

Contrasting PPS with EPS conditions revealed significant activations within the parietal cortex, with peak responses localized in the rostral part of the IPL, in the SPL, and in the postcentral gyrus partly overlapping with the aIPS. This pattern of activations is consistent with extensive literature linking these parietal regions to near-space coding (Basile et al., 2024; Cléry et al., 2015; Grivaz et al., 2017; Rizzolatti et al., 1997) and the representation of action-related information, including manipulable objects (Culham & Valeyear, 2006; Peeters et al., 2009; Van Overwalle & Baetens, 2009). Although bilateral parietal engagement was observed, the predominantly right-lateralized activation pattern aligns with right-hemisphere dominance in spatial coding and body-space representation (Harris, 2000; Longo et al., 2015; de Jong et al., 2001; Schintu et al., 2014; Daprati et al., 2010). While this has been frequently observed in previous research (Basile et al., 2024), no significant contralateral premotor activation was found in the present study. This lack of activation may be related to the reduced premotor recruitment often observed in tasks that do not require overt motor execution (Bartolo et al., 2014b; Grivaz et al., 2017), possibly due to rapid adaptation of premotor neurons to static visual stimuli (Rizzolatti et al., 1981). Alternatively, it is also possible that sub-threshold premotor activity was insufficient to reach statistical significance, in line with the high incidence of type-II errors commonly reported in fMRI studies (Lieberman & Cunningham, 2009).

Ownership exerted a significant influence on spatial encoding in PPS. Reachability judgements involving self-owned objects recruited a robust, right-lateralized parietal cluster, along with activations in the rIFG. The rIFG is frequently linked to the general recruitment of executive control (Miller & Cohen, 2001), including visuospatial working memory (Geers et al., 2021; Rämä & Sala, 2001) and early-stage inhibitory control (Aron & Poldrack, 2006). These findings converge

with prior reports of enhanced executive control in decisions involving self-owned objects within PPS (Lenglart et al., 2024). In contrast, reachability judgements involving other-owned objects elicited a more localized parietal response and were associated with increased activation in the pre-SMA. The pre-SMA is engaged in late-stage motor inhibition (Nachev et al., 2007; Obeso et al., 2013) and has been suggested to play a role in the suppression of goal-incongruent motor actions (Cunnington et al., 2005). Its activation in response to other-owned objects in PPS may reflect an inhibitory mechanism that prevents actions inconsistent with social norms or personal goals, such as initiating movement toward objects belonging to others.

In contrast to PPS, reachability judgements for objects located in EPS did not evoke parietal activation, consistent with previous studies (Bartolo et al., 2014b). However, a key finding was that processing objects in EPS was associated with widespread engagement of the prefrontal cortex. While perception of stimuli in EPS, unlike in PPS, is not typically marked by specific neural activations (Bartolo et al., 2014b), the proximity of objects to a virtual character in EPS may have altered the weight attributed to the social context. This, in turn, led to prominent activity in the medial prefrontal cortex, encompassing regions typically linked to both self-referential cognition and social reasoning (de la Vega et al., 2016; Lieberman et al., 2019; Lockwood et al., 2018).

This social influence was further modulated by ownership: detailed contrasts between EPS and PPS for self- and other-owned objects revealed overlapping yet distinct activation profiles. Self-owned objects preferentially engaged a large prefrontal cluster, including both the vmPFC and dmPFC, while other-owned objects predominantly activated the vmPFC and the right posterior superior temporal sulcus (pSTS). The pSTS is a key region for social perception (Isik et al., 2017), particularly in interpreting others' actions and intentions (Chakrabarti & Baron-Cohen, 2006).

Moreover, it has been proposed to play a role in linking contextual and perceptual information in social action-related scenarios (Stehr et al., 2021). Its preferential activation by other-owned objects near a virtual character may, therefore, reflect the integration of perceptual and inferential processes for interpreting the social significance of those items.

#### Fronto-parietal recruitment as a function of ownership

To test the hypothesis that fronto-parietal activations are sensitive to object ownership, we conducted a targeted analysis within this network, revealing enhanced bilateral recruitment of parietal areas when participants evaluated self-owned stimuli in PPS. The absence of preferential activation for other-owned objects further underscores the asymmetrical coding of ownership within this network, with a preferential engagement of the core PPS network in processing relevant targets. In contrast, in EPS, self-owned objects did not elicit significant activation, while otherowned objects selectively engaged the right parietal cortex. This region is recognized as part of the mirror neuron system (Rizzolatti & Rozzi, 2018) and has previously been implicated as a key node within a "social brain network", supporting action understanding and social coordination (Gallese et al., 2002; Fujii et al., 2007; Preston & Newport, 2008). These findings lend support to recent models of PPS as selectively tuned to integrate spatial and bodily information based on contextual cues, particularly when they hold relevance for potential interaction. Such contextdependent recruitment of the fronto-parietal network aligns with recent behavioral accounts highlighting the influence of social factors on PPS-related processing in relation to both objects' affordances and social norms (Lenglart et al., 2023; Patané et al., 2021).

# Object ownership in the medial prefrontal cortex

#### 7.2.4. Discussion

A central objective of the present study was to determine how self-relevant brain regions, specifically the vmPFC and dmPFC, encode object ownership in relation to spatial context. While univariate analyses yielded no significant ownership effect in PPS, multivoxel pattern analysis (MVPA) uncovered finer-grained distinctions. The vmPFC discriminated self-owned objects above chance in PPS, but failed to differentiate between self- and other-owned objects in EPS. This suggests that vmPFC activity does not reflect an inherent or fixed self-preference, but instead functions as a context-sensitive filter, tagging self-relevant stimuli when they are situationally or motivationally pertinent. This interpretation aligns with recent models that conceptualized the vmPFC not as an amodal "self-hub", but as a dynamic, context-dependent filter of self-relevant information (Lieberman et al., 2019; Schäfer & Frings, 2019).

In contrast, the dmPFC demonstrated consistent sensitivity to self-ownership across space, with accurate classification performance for self-owned objects in both PPS and EPS. This suggests that the dmPFC hosts neural populations that support more enduring self-related information within a social context (Katsumi et al., 2024), independently of immediate behavioral relevance. Alternatively, or additionally, rather than encoding the "self" per se, the dmPFC could track the relational status of an object in a social context ("belonging to me" vs. "belonging to another") and help maintain the distinction between items relevant to the self and those relevant to others. This interpretation aligns with a body of work linking the dmPFC to social comparison, self-other differentiation, and social inferential evaluation (D'Argembeau et al., 2007; Piva et al., 2019). Under this view, the dmPFC may sustain ownership-related distinctions even when behavioral relevance is low, as these distinctions are crucial for guiding social behaviour and cooperation.

Overall, a key finding of the present study is that the engagement of the vmPFC in self-referential processing seems to be constrained by the spatial configuration of the environment in relation to action. This aligns with studies suggesting that transient disruption of the vmPFC does not typically abolish self-reference effects (Schäfer & Frings, 2019). Notably, the vmPFC ROI in the present study largely corresponds to clusters identified in reverse-inference analysis by Lieberman et al. (2019), which primarily code for affective and situational processing. In contrast, the dmPFC ROI overlaps with clusters linked to self-related and social processing. These distinctions are further supported by recent evidence highlighting the role of the vmPFC in processing reward-related or motivational information, and of the dmPFC in tracking social information related to social conformity (Su et al., 2025). Taken together, these findings suggest that the vmPFC flexibly tags self-relevant stimuli with motivational value and behavioral relevance depending on context, while the dmPFC supports a sustained representation of self-related information within social contexts, particularly in relation to the role of object ownership in structuring appropriate social interaction.

## 7.2.5. Conclusion

In sum, our findings demonstrate that the neural encoding of PPS and EPS is not uniform, but is modulated by the contextual factor of object ownership. Parietal regions traditionally associated with near-space and action-related processing were preferentially engaged when participants evaluated self-owned objects within PPS, whereas other-owned objects elicited a more restricted parietal response and recruited the pre-SMA. In EPS, ownership modulated the activity of prefrontal regions involved in social cognition and self-related processing, notably the vmPFC and dmPFC. Crucially, MPVA classification analyses revealed that vmPFC coding for self-

ownership was contingent upon spatial proximity, reflecting a sensitivity to behavioral relevance, whereas the dmPFC maintained a stable representation of self-ownership across both PPS and EPS. Together, these results challenge models that propose a unitary, centralized mechanism for self-ownership or self-relevance. Instead, they support a distributed context-sensitive framework in which behavioral and social factors shape neural processing as a function of space.

#### 7.2.6. *Method*

## **Participants**

Twenty-five right-handed healthy volunteers took part in the study. The data of three participant were removed because of technical issues (1 participant) or excessive movement-induced noise (2 participants), computed as follows: if excluded volume > 4 minutes mean, if FD > 0.3 mm, or if more than 20% of FDs > 0.5 mm or > 1.5 times the derivative of the RMS variance (following the recommendations of Satterthwaite et al., 2013, and as implemented in fMRIPrep). Ultimately, the data of 22 participants were analysed (14 female,  $m_{age} = 21.51$ ,  $SD_{age} = 3.72$ ). All participants had normal or corrected-to-normal vision, had no history of neurological or psychiatric disorder, and gave their formal written consent before taking part in the study. The experimental design was approved by the local ethics committee (reference CEICSH 114/2023), in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki, 2013).

## Materials and procedure

Before entering the scanner, participants chose a colored paper cup among two (blue or yellow) in order to induce object ownership. They were told that the chosen paper cup was theirs

and that they could keep it even after the experiment, and the non-chosen one belonged to a virtual character they would meet later. Both pre-experimental and experimental tasks used a virtual environment designed with Unity (version 2021.3.13f1) composed of a virtual table of 150 cm long with a 3D wood texture, at the extremity of which a neutral-faced virtual character taken from the ATHOS database (Cartaud & Coello, 2020) was seated (Figure 31.A). No spatial cue biasing the perception of distance or allowing for the development of strategies by participants was available in the virtual environment. The two paper cups were replicated in the virtual environment and designed to be isoluminant in Unity, with a luminance value of 100% (HSV), and maintained a comparable contrast ratio against the virtual table (yellow cup to table ratio: 1:6.36; blue cup to table ratio: 1:6.08). The virtual environment was displayed through a monitor screen placed in front of the MRI scanner visible through mirrors set at the MRI-head coil.

# Pre-experimental session

To account for inter-individual variability in the perception of distance in a virtual environment, participants performed a pre-experimental task where a neutral grey cup (i.e., with no ownership, figure 31.B) was randomly presented at 29 distances ranging from 5 to 145 cm from the proximal edge of the virtual table. For each trial, participants were asked to estimate if they would be able to reach the cup with their right hand without moving their shoulders or their trunk; no real movement was allowed. They provided their responses by pressing buttons on a response grip with their left index and thumb. At the end of this task, a reachability threshold was obtained by the computer for each participant using the formula:

$$y = (exp(\alpha + \beta x))/(1 + exp(\alpha + \beta x))$$

#### 7.2.6. Method

where x represents the distance of the cup on the table and y represents the participant's probability of estimating the cup as "reachable". The reachability threshold was obtained by computing  $-\alpha/\beta$  and served afterwards to segment, for each participant, the table into a PPS and EPS region.

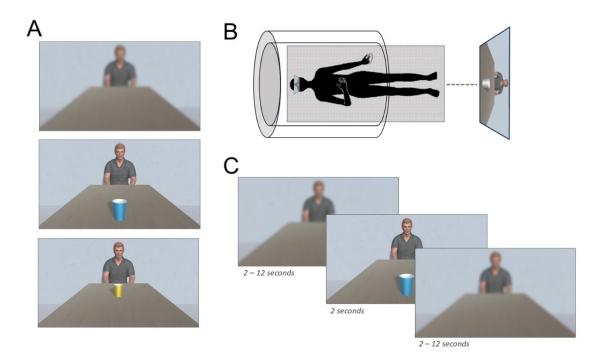


Figure 31. (A) Illustration of the virtual environment with the blurred mask (top panel), with a cup located in the participant's peripersonal space (middle panel) or extrapersonal space (bottom panel). (B) Schematic representation of the experimental setup during the pre-experimental session. (C) Time-course of stimuli presentation.

## Experimental session

In this task, a mask consisting of a Gaussian blur was applied to the virtual environment with no cup on the table and presented for a jittered period of 2 to 12 s (Figure 31.C). Subsequently, one of the two cups (yellow or blue) was individually presented for 2 s either in the PPS (at -70%, -60%, or -50% from the previously computed reachability threshold), in the EPS (at +50%, +60%,

and +70% from the previously calculated reachability threshold) or, to enhance the complexity of the task, near the reachability threshold in 10% of the trials, used as fillers (at -10%, 0% and +10% of the reachability threshold). Participants were instructed to imagine themselves seated at the table within the virtual environment, and to passively estimate whether self- and other-owned cups (yellow and blue) positioned at varying distances would be reachable with their right hand. They were explicitly instructed to make these reachability judgments solely from their own perspective and not from the viewpoint of the virtual character in front of them. To maintain engagement while minimizing the influence of motor preparation-related activations, participants were requested to respond only in 10% of the trials, specifically when a question mark appeared on the screen.

# fMRI data acquisition and pre-processing

All fMRI data were acquired using a 3T Siemens Magnetom Trio scanner (Siemens, Erlangen, Germany) and an 8-channel receive-only head coil equipped with a mirror. Blood oxygen level-dependent-sensitive (BOLD) fMRI images were acquired in an interleaved way through use of an T2\* weighted echo-planar images (EPIs) (TR = 2000 ms, TE = 18 ms, FA = 85°, Field of View (FoV) = 200 mm × 200 mm, matrix size =  $66 \times 66$ , in-plane resolution = 3.03 mm  $\times 3.03$  mm) from 48 axial slices of 3-mm thickness with 3-mm interslice gap, covering the whole brain. A total of 730 volumes were acquired during the task. One structural T1-weighted images were collected (TR = 2400 ms, TE = 2.53 ms, FoV = 25.5 mm  $\times 25.5$  mm, matrix size =  $256 \times 256$ , in-plane resolution = 0.98 mm  $\times 0.98$  mm) and used to project the functional maps. Participants were instructed to refrain from moving to reduce movement artifacts, and head motion was minimized using ear pads.

#### 7.2.6. Method

Results included in this manuscript come from preprocessing performed using fMRIPrep 23.2.0 (Esteban et al. (2019); RRID:SCR\_016216), which is based on Nipype 1.8.6 (Gorgolewski et al. (2011); RRID:SCR\_002502). A comprehensive description of the preprocessing procedure for both anatomical and functional imaging data can be found in Appendix n°2, section 9.2.

# fMRI analysis

Pre-processed functional imaging data were analysed using Statistical Parametric Mapping (SPM12, Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB R2024b (MathWorks Inc., Natick, MA, USA). For each participant, a first-level analysis was conducted using a General Linear Model (GLM) to estimate the hemodynamic response for each condition of interest. To optimize denoising while minimizing the risk of spurious signal influencing the results (Ciric et al., 2017), 36 regressors of non-interest resulting from 3D head motion estimation (x, y, z translation and three axes of rotation, their derivatives, quadratic terms, and squares of derivatives) to which were added k spike regressors (as in Satterthwaite et al., 2013 and as implemented in fMRIPrep) were added in the design matrix. A 2×2 factorial design was employed, with two factors each with two levels: Space (Peripersonal, Extrapersonal) and Ownership (Self, Other).

## Univariate analysis

We first conducted a whole-brain analysis to obtain an examination of global neural activations to the experimental conditions. A F-contrast first assessed the interaction of Space and Ownership. Then, t-contrasts were computed to examine the main effects of Space (PPS > EPS, EPS > PPS) and Ownership (Self > Other, Other > Self). To gain a deeper understanding of how spatial neural processing varies with object ownership, we computed t-contrasts comparing PPS

and EPS for self- and other-owned objects (PPS-Self) EPS-Self; EPS-Self; EPS-Self; PPS-Other > EPS-Other; EPS-Other > PPS-Other). Individual t-contrast images were generated for each participant before being entered into a one-sample t-test for second-level analyses. Voxel significance was thresholded at p < 0.001 (uncorrected; Woo et al., 2014), with clusters considered as significant at p < 0.05 (FDR-corrected; Genovese et al., 2002).

To assess whether brain regions typically involved in processing stimuli in PPS were modulated by object ownership, we computed additional t-contrasts comparing Self- and Otherowned objects within the PPS (PPS-Self > PPS-Other, PPS-Other > PPS-Self). Based on the wellestablished role of the fronto-parietal network in PPS processing (Rizzolatti et al., 1997; Cléry et al., 2015), we selected regions of interest (ROIs) from Grivaz et al. (2017), including the postcentral and precentral gyri, supramarginal gyrus, and superior and inferior parietal lobules. Analyses were restricted to this core PPS network using the ROI analysis implemented in the WFU PickAtlas toolbox in SPM12. As studies have suggested that observing actions or objects related to a conspecific can activate the observer's fronto-parietal network (Costantini et al., 2011; Kilner et al., 2007; Rizzolatti & Sinigaglia, 2010), we additionally investigated whether ownershiprelated effects extend near the virtual character by performing analogous contrasts in the EPS (EPS-Self > EPS-Other, EPS-Other > EPS-Self). Given our a priori hypotheses and the subtle nature of PPS-related sensorimotor activations (Bartolo et al., 2014b; Grivaz et al., 2017), we applied a more liberal statistical threshold (voxel-wise p < 0.005 uncorrected, cluster-level p < 0.05 FDR-corrected, Bartolo et al., 2014b).

All coordinates are reported in MNI-152 space and anatomical labels were assigned using the Automated Anatomical Labelling (AAL) atlas, version 3v1 (Rolls et al., 2020). When available, cytoarchitectonic location was derived from the JuBrain Anatomy Toolbox (Eickhoff et al., 2007).

For regions not covered by the cytoarchitectonic maps, Brodmann area (BA) designations were provided.

#### Multivariate analysis

Given the ongoing debate about the distinct roles of the dorsal and ventral mPFC in processing self- and other-related contextual information, we aimed to determine whether activation patterns in this region, if observed, were context-dependent. To examine this, and given that univariate studies frequently report overlapping activation in the mPFC for self- and otherrelated processing, we employed multivariate pattern analysis (MVPA) to investigate whether distinct multivoxel patterns could differentiate these processes. MVPA analyses spatial patterns of neural activity and voxel relationships, enabling the detection of subtle, context-specific neural representations. Unlike methods that assess overall activation, MVPA thus captures fine-grained spatial patterns that reflect feature-selective neural populations. Regions of interest (ROIs) were defined a priori using the AAL atlas in the WFU PickAtlas toolbox in SPM12. The ventral mPFC ROI was defined as a binary mask encompassing the orbital superior and inferior frontal gyri and the gyrus rectus, while the dorsal mPFC ROI was defined as the superior medial gyrus. MVPA was conducted using The Decoding Toolbox (v3.999) in MATLAB, with beta images derived from the general linear model (GLM) on unsmoothed data. These beta-values were input into ROI-based MVPA classifiers, using a leave-one-subject-out (LOSO) cross-validation procedure to minimize overfitting and identify shared patterns across individuals. A linear support vector machine (SVM) classifier was trained on data from 21 participants, while the data from the remaining participant served as the test set. This LOSO cross-validation procedure was iteratively repeated such that each participant was used once as the test subject. Null confusion matrices were generated by

randomly shuffling the pattern labels of the training and testing data within-subject 1000 times, and Bonferroni-corrected p-values were calculated based on the obtained distributions.

# 7.2.7. *Tables*

Table 2. Brain regions showing significant activations for (a) the contrast between peripersonal space and extrapersonal space and (b) the contrast between extrapersonal and peripersonal space. x, y, z = peak coordinates (MNI); T = t-statistic.

				Peak-leve	el			Cluster-level	
Macroanatomical location	Microanatomical composition	X	у	Z	T	Р	Number of voxels	P uncorrected	P FDR
PPS – EPS									
Left and right calcarine sulcus,	hOc1 (V1) (37,3%),	-8	-84	-3	7.48	0	303	0	0
Lingual gyrus	hOc2 (V2) (14,7%), hOc3v (V3v) (12,8%),	4	-84	-6	6.45	0			
	hOc4v (V4v) (9.7%),	16	-99	6	6.26	0			
Right inferior parietal lobule,	hIP3 (IPS) (12.7%),	49	-44	54	6.47	0	313	0	0
Superior parietal lobule, Postcentral gyrus	PFm (IPL) (9.2%), area 1 (7.9%),	40	-44	51	6.15	0			
hIP2 (IPS) (7.5%)	· //	28	-87	24	6.01	0			
Right cuneus,	Area 7P (SPL) (41.1%),	19	-68	45	6	0	89	0	0
Precuneus, Superior parietal lobule,	Area 7A (SPL) (4.0%)	7	-77	57	5.34	0			
Superior occipital gyrus		13	-68	66	4.13	0			
Left middle occipital gyrus, Superior occipital gyrus	hOc3d (V3d) (38%), hOc4p (22.8%), hOc4d (V3a) (16.8%), hOc1 (7.1%)	-23	-93	12	5.93	0	48	0.001	0.011
Right pars opercularis, Middle frontal gyrus, Pars triangularis	BA44	40	13	33	5.22	0	62	0	0.003
Left supplementary motor area,	6mr, pre-SMA (37.4%)	7	13	54	5.04	0	45	0.001	0.016
Right supplementary motor area		-8	10	57	4.92	0			

Left superior parietal lobule,	hIP3 (IPS) (26%),	-26	-53	45	4.84	0	72	0	0.001
Inferior parietal lobule	hIP2 (IPS) (14%), 7A (SPL) (10.3%),	-44	-47	51	4.83	0			
	area PFm (IPL) (7.6%)	-26	-53	57	4.3	0			
S-PPS									
Left superior frontal gyrus,	BA8	-11	38	54	8.13	0	91	0	0
Medial frontal gyrus		-23	32	57	5.83	0			
		-26	38	51	5.5	0			
Left frontal middle orbital,	p32 (29.2%),	-5	56	-3	7.17	0	643	0	0
Frontal superior medial, Anterior cingulate cortex (pregenual)	Fp2 (18.4%)	7	56	12	6.45	0			
Right medial orbital cortex		-5	53	6	5.75	0			
Left paracentral lobule,	4a (22.7%),	-3	-23	75	6.65	0	44	0.001	0.011
SMA, Postcentral gyrus	BA6	-14	-32	78	5.35	0			
Right paracentral lobule		7	-17	78	4.03	0			
Left superior frontal gyrus,	Fp1 (10.8%),	-23	59	24	5.52	0	40	0.001	0.011
Middle frontal gyrus	BA10	-20	62	12	3.99	0			
Right temporal superior gyrus, Supramarginal gyrus	TE3 (20.2%), PFcm (IPL (17.4%), PF (IPL) (13.4%)	65	59	12	4.97	0	24	0.009	0.042
Left lingual gyrus, Occipital inferior gyrus, Cerebellum crus 1	hOc3v (72.7%), hOc2 (19.8%), hOc4v (7.1%)	-20	-93	-15	4.89	0	39	0.001	0.011
Left temporal middle gyrus, Temporal superior gyrus	TE3 (24.3%), BA21	-63	-8	-9	4.87	0	29	0.005	0.029
Right lingual gyrus,	hOc3v (75.6%),	19	-93	12	4.73	0	24	0.009	0.042

# 7.2.7. Tables

Inferior occipital gyrus, hOc2 (23.8%) Calcarine sulcus

Table 3. Brain regions showing significant activations for the contrast between all factors. x, y, z = peak coordinates (MNI); F = f-statistic.

				Peak-le	vel			Cluster-level	
Macroanatomical location	Microanatomical composition	x	у	Z	F	Р	Number of voxels	P uncorrected	$P_{FDR}$
Interaction									
Left superior frontal gyrus,	BA10	-23	59	6	37.8	0	44	0	0.003
middle frontal gyrus, medial superior frontal gyrus		-23	56	18	25.3	0			
Left superior frontal gyrus	Area Fp1(29.5%),	-20	47	45	27.8	0	46	0	0.003
	BA8	-23	35	48	21.3	0			
		-23	26	45	18.1	0			

Table 4. Brain regions showing significant activations for (a) the contrast between peripersonal space and extrapersonal space for self-owned objects and (b) the contrast between peripersonal space and extrapersonal space for other-owned objects. x, y, z = peak coordinates (MNI); T = t-statistic.

		Peak-le	evel				Cluster-level		
Macroanatomical location	Microanatomical composition	x	у	Z	T	P	Number of voxels	P uncorrected	$P_{FDR}$
PPS Self – EPS Self									
Left calcarine sulcus, Lingual gyrus	hOc1 (V1) (30.1%), hOc3v (V3v) (20.2%),	-5	-84	-3	8.22	0	227	0	0
Dingual gyrus	hOc4v (V4v) (13.8%), hOc2 (V2) (11.6%)	-23	-71	-12	8.82	0			
	11002 (72) (11.070)	-14	-74	-9	8.63	0			

Left middle occipital gyrus, Superior occipital gyrus	hOc3d (v3d) (37.3%), hOc4lp (25.2%), hOc4d (V3A) (14.4%), hOc1 (V1) (9.0%)	-23	-96	9	7.33	0	24	0	0.001
Right postcentral gyrus, Inferior parietal lobule,	hIP3 (IPS) (14.7%), 7A (SPL) (11.5%),	55	-32	57	6.3	0	246	0	0
Superior parietal lobule,	PFm (IPL) (10.1%),	40	-41	51	5.37	0			
Supramarginal gyrus	Area 1 (7.4%), Area hIP2 (IPS) (7.2%)	37	-56	48	5.1	0			
Right inferior frontal operculum,	Area 44 (71.9%)	59	10	21	5.97	0	41	0.001	0.009
Precentral gyrus, Pars triangularis		55	16	12	5.82	0			
Right calcarine sulcus, Cuneus,	hOc1 (v1) (43.5%) hOc2 (v2) (24.0%)	13	-99	6	5.67	0	36	0.002	0.013
Superior occipital gyrus	hOc3d (V3d) (15.6%) hOc3v (V3v) (3.4%)	22	-99	15	4.48	0			
PPS other – EPS other									
Left and right medial superior	Area 6mr / preSMA	4	29	51	6.3	0	60	0	0.005
frontal gyrus, Supplementary motor area	(10.1%), BA8, BA6	7	13	51	4.12	0			
		-8	13	51	3.98	0			
Right inferior parietal lobule,	hIP3 (IPS) (35.0%),	46	-44	51	5.72		42	0.001	0.01
Superior parietal lobule, Supramarginal gyrus	hIP2 (IPS) (32.0%), PFm (IPL) (23.1%), hIP1 (IPS) (2.7%)					0			
Right calcarine sulcus,	hOC1 (V1) (57.2%),	16	-99	6	5.53		29	0.004	0.036
Cuneus, Superior occipital gyrus.	hOc3d (V3d) (6.5%), hOc2 (V2) (5.7%)					0			

# 7.2.7. Tables

Left calcarine sulcus,	hOc1 (V1) (69.2%),	-8	-87	-3	5.44		45	0.001	0.01
Lingual gyrus,	hOc2 (V2) (18.7%)					0			
Middle occipital gyrus		1	-74	0	4.07				

Table 5. Brain regions showing significant activations for (a) the contrast between extrapersonal space and peripersonal space for self-owned objects and (b) the contrast between extrapersonal space and peripersonal space for other-owned objects. x, y, z = peak coordinates (MNI); T = t-statistic.

				Peak-le	evel		Cluster-level			
Macroanatomical location	Microanatomical composition	х	у	z	T	P	Number of voxels	P uncorrected	$P_{FDR}$	
EPS Self – PPS Self										
Left superior frontal gyrus,	Area Fp1 (30.6%)	-17	62	15	7.62	0	933	0	0	
Medial superior frontal gyrus	BA10, BA8, BA9	-20	56	21	6.61	0				
		-23	38	48	6.54	0				
Left superior temporal gyrus,	Area TE3 (8,4%)	-57	-8	-3	5.79	0	39	0.001	0.015	
Middle temporal gyrus, Rolandic operculum	BA22, BA21	-44	-5	-9	4.75					
		-66	-8	-9	4.72					
Left and right midcingulate cortex,	Area 6mc / SMA (15,3%)	7	-8	45	5.1	0	31	0.003	0.019	
Right supplementary motor area	BA24	16	-2	45	4.09					
Left paracentral lobule,	Area 4a (12%),	-14	-32	78	5.02	0	33	0.003	0.018	
Postcentral gyrus	Area 5 L (4,8%) BA2, BA4	-26	-26	75	3.84					
Left precuneus,	7A (6,2%)	-2	-59	45	4.99	0	39	0.001	0.015	
Right precuneus	BA7	-5	-59	36	4.47					

Left lingual gyrus, Inferior occipital gyrus	hPc3V (V3v), (75,8%), hOc4lp (13,2%), hOc2 (V2) (9,2%)	-17	-93	-15	4.66	0	36	0.002	0,16
EPS Other – PPS Other									
Left superior frontal gyrus,	Area Fp2 (42.8%),	-5	59	0	5.22	0	109	0	0
Medial superior frontal gyrus, Orbital gyrus,	Area p32 (14.9%)	-2	65	6	5.18	0			
Pregenual anterior cingulate cortex		1	47	-3	4.34	0			
Right superior temporal gyrus, rolandic	Area OP4 (PV) (38.2%),	68	-20	9	5.09	0	62	0	0.001
operculum	Area TE3 (22.5%), Area TE 1,2 (2.8%),	65	1	0	4.26	0			
		68	-8	15	4.22	0			
Left and right cuneus	Area hOc3d (V3d) (41.9%), Area hOc4d (V3A) (22.5%), Area hOc2 (V2) (12.6%)	7	-87	33	4.72	0	35	0.002	0.017

Table 6. Brain regions showing significant activations for (a) the contrast between self-owned and other-owned objects in peripersonal space and (b) the contrast between other-owned and self-owned objects in extrapersonal space for other-owned objects, restricted to a ROI composed of the fronto-parietal network subtending processing in PPS (Grivaz et al., 2017). x, y, z = peak coordinates (MNI); T = t-statistic.

				Peak-le	evel		Cluster-level			
Macroanatomical location	Microanatomical composition	x	у	Z	T	P	Number of voxels	P uncorrected	$P_{FDR}$	
PPS Self > PPS Other										
Right inferior parietal lobule, Superior parietal lobule,	Area 1 (39.5%), Area 2 (14.3%),	52	-35	57	4.01	0	36	0.017	0.047	

7.2.7. Tables

Postcentral gyrus	Area of (ipl) (10.2%)								
Left inferior parietal lobule, Supramarginal gyrus, Postcentral gyrus	PFt (IPL) (78.5%), PFop (IPL) (10.6%), Area 2 (6.5%)	-57	-26	45	3.52	0	30	0.026	0.047
EPS Other > EPS Self									
	hIP3 (IPS) (24.5%),	37	-53	45	3.63	0	116	0	0.002
Right angular gyrus, Supramarginal gyrus	hIP2 (IPS) (18.9%), hIP1 (IPS) (17.0%),	46	-41	51	3.45	0			
	PFm (IPL) (14.1%)	34	-47	39	3.42	0			

# 7.3. SEARCHING FOR DIRECT EVIDENCE OF THE EMBODIMENT OF OWNERSHIP WITHIN THE SENSORIMOTOR SYSTEM

The fMRI findings showed that activations of parietal regions of the fronto-parietal network encoding objects in PPS were sensitive to object ownership. In this respect, it is possible to suppose that the recruitment of the motor system in response to graspable objects is modulated or suppressed when the object belongs to someone else. Thus, we interpreted ownership was a social modulator participating in the preparation of relevant action for oneself in the environment. Such results are consistent with embodied theories of cognition and, as Constable et al. (2011) proposed, ownership seem to be embodied within the sensorimotor system. As they propose, "the action system [could be] blind to the potential for action towards another person's property". The affordances offered by objects belonging to others may therefore be inhibited (or, as they propose, not perceived): when an object is not ours to act upon, its potential for action may be suppressed at the level of motor representation. In situations where the object is located within PPS but rendered socially unavailable due to ownership constraints, the cognitive system may resolve the conflict between physical availability and social inaccessibility by dampening the motor system's excitability in response to other-owned objects.

This interpretation is coherent with the modulation of parietal activation driven by ownership reported in the fMRI study, which suggests that ownership biases action planning upstream of execution. To test this hypothesis directly, we designed a TMS experiment where single pulse was delivered over the primary motor cortex (M1) while participants viewed objects labelled as self-or other-owned. Indeed, previous studies using single-pulse TMS over M1 (e.g. Cardellicchio et al., 2011, 2013) have shown that such stimulation can reveal early recruitment of motor networks during the passive perception of objects that are physically reachable. This corticospinal excitability is interpreted as a marker of the motor system's preparation for potential action, even

## 7.2.7. Tables

in the absence of any movement. Therefore, beyond removing the confound of behavioral response, showing that self-owned objects elicit stronger M1 excitability than other-owned objects would provide direct evidence that ownership is embodied as a sensorimotor constraint in the processing of objects for action.

Part III
DISCUSSION

#### 8. DISCUSSION

#### 8.1. SUMMARY OF THE THESIS

#### 8.1.1. Summary of the theoretical background

The studies presented in the empirical section of this thesis are grounded in a theoretical framework that integrates two key constructs: peripersonal space (PPS) and object ownership, proposed as neurocognitive mechanisms that jointly modulate how space and objects are represented in the vicinity of the body. This background offers a functionally rooted approach to understand how the encoding of the space surrounding the body, and the processing of objects in this space, are modulated by the social and personal significance of the objects it contains.

The first construct, PPS, refers to the region of space immediately surrounding the body within which physical interactions are directly possible. Contemporary models describe PPS as a flexible and context-sensitive interface that supports both defensive and goal-directed behaviours, that is, all actions aiming at creating or avoiding contact between an element of the environment and the body (de Vignemont & Farnè, 2024; Bufacchi & Iannetti, 2018). PPS thus follows a gradient anchored in action potential, and its boundaries vary as a function of the physical and social environment, and of the disposition of the body (Cléry et al., 2015; Di Pellegrino & Làdavas, 2015). In line with this framework, neurophysiological studies have shown that multisensory neurons in premotor and parietal regions code for stimuli near the body and that their receptive fields adapt following limb configuration for action planning (Avillac et al., 2005; Fogassi et al., 1996; Rizzolatti et al., 1981a, b, c).

Besides, object ownership has emerged as a powerful contextual cue for self-relevance, capable of modulating perceptual and cognitive processes. Indeed, ownership signals not only a social relationship (i.e., pointing out who has control over an item), but also an extension of the

self into the environment (Belk, 1988; James, 1890; Morewedge, 2021). This incorporation of owned objects into the concept of self gives rise to well-documented biases in cognitive processes, such as attention and memory, referred generally to as self-prioritization effects (Cunningham & Turk, 2017; Sui et al., 2012). To corroborate these findings, neuroimaging studies showed that self-owned objects recruit the medial prefrontal cortex (mPFC), especially its ventral subdivision, which has been proposed to signal the personal relevance of external stimuli (Denny et al., 2012; Kim & Johnson, 2012; Lockwood et al., 2018). Yet, recent accounts emphasize that such effects are not automatic: they depend on many additional factors, such as relevance to the task, context, and instructions (Golubickis & Macrae, 2023).

The central question guiding the present thesis was thus to understand the interplay between ownership and space in object processing. Although it was possible that these two aspects biases objects processing separately, and that, for instance, self-ownership biases consistently object processing across space, I hypothesized that self-owned objects receive prioritized processing specifically when they are situated in PPS, where direct interaction is possible and socially appropriate. In this proposition, the sensorimotor processing of objects in PPS is modulated by its social and conceptual attributes, which challenges models that isolate the self-relevant aspect of ownership and interpret it as a purely attentional bias. Instead, this hypothesis suggests that ownership has a functional role as it modulates the spatial encoding of objects within an embodied and action-oriented framework.

To answer these questions, the empirical studies presented in this thesis explored how ownership affects the representation of PPS and the processing of objects within its boundaries. In this context, we used a reachability judgement task as it is known to capture the sensorimotor

### 8.1. Summary of the thesis

dimension of object processing in PPS (Bartolo et al., 2014b; Wamain et al., 2016), rather than mainly perceptual or attentional processes (Geers & Coello, 2023, Submitted; Zanini et al., 2021).

# 8.1.2. Summary of the experimental work

In chapter 4, the first experiment investigated how ownership influences the representation and processing of objects in PPS from a behavioral perspective. Participants selected a mug as being their own, while another mug was assigned to a virtual character visible in the virtual environment. Participants then estimated whether these two mugs were reachable when placed at different distances on a virtual table. Response times in this reachability judgement task were significantly faster for self-owned compared to other-owned mugs, but only when they were located in the PPS. In the EPS, this advantage disappeared. Moreover, reachability judgments were biased: participants estimated that they could reach their mug at farther distances compared to the other's mug, resulting in an extension of the PPS boundary when considering self-owned objects. Interestingly, this expansion was correlated with scores of the Fantasy subscale of the IRI (Davis, 1983), suggesting that individuals with a higher facility to engage in imaginary or virtual situations were more susceptible to biases related to our experimental manipulation. After each judgement, participants localized where the mug was placed, while the virtual character was covertly shifted spatially. Localization errors occurred predominantly for objects in the EPS regardless of ownership, implying that attentional focus at a farther distance induced a shift from an egocentric to an allocentric frame of reference. In sum, this chapter provides clear evidence that self-owned objects in PPS benefit from a prioritized processing: actions toward self-owned mugs are planned more quickly, and the peripersonal boundary expands to when they are the available stimuli.

In chapter 5, the second experiment used surface electromyography (EMG) to examine the influence of ownership on motor control through executive inhibition. We recorded muscle activity

from the thumb in an adapted reachability judgement task to detect early motor activations and track error correction. EMG recordings also allowed us to investigate the proportion of partial errors (i.e., small erroneous activations that were corrected online) as an index of inhibition control efficiency. For objects in the PPS, correct responses identified to self-owned cups, from muscle activity, were initiated on average faster than to other-owned cups, confirming results found in the first experiment. Conversely, in the EPS, the trend reversed (other-owned objects initiated slightly shorter latencies than self-owned objects, though overall responses were slower in EPS). This pattern was also found in the behavioral RTs, indicating that spatial location and ownership interact to shape both motor initiations and responses. Interestingly, a time-based analysis of initiated errors (wrong responses according to the spatial position of the stimulus) revealed that the difference in error frequency between self- and other-owned objects in both PPS and EPS was not attributable to rapid and impulsive responses. Rather, the divergence increased over time, suggesting a progressive and accumulating influence of ownership: as the response windows unfolded, participants appeared increasingly biased toward ownership-related inhibition, which thus seems a robust phenomenon. However, most errors initiated were corrected online, and motor correction was significantly more efficient and rapid for self-owned compared to other-owned objects in the PPS, while this effect was not observed in the EPS. This suggests stronger recruitment of rapid inhibitory and adjustment processes for self-relevant stimuli in the PPS. As a whole, in this study, the presence of a "mirror pattern" in a number of measures (i.e., faster responses for other-owned objects in the EPS) suggests a spatial trade-off: each target preferentially aligns with the relevant agent's action space (self in PPS, other in the EPS). However, the fact that self-owned objects in PPS yield more efficient corrections indicates a robust PPS self-advantage at early stages of motor control.

### 8.1. Summary of the thesis

In chapter 6, we used electroencephalography (EEG) recordings to track the time course of object processing in the PPS vs. EPS as a function of ownership. Participants again performed the reachability judgement task with self-owned and other-owned objects while facing a virtual character. The ERP revealed a clear temporal stratification: early perceptual (N1) and sensorimotor (anterior N2) were sensitive to the object's spatial location, but not to ownership, with respectively earlier and larger components for objects in the PPS than in the EPS. In contrast, mid- to late-latency ERPs reflected social content through ownership. The P3 component was enhanced for self-owned objects (but only in the PPS), and an anterior N400-like negativity, which typically indexes semantic or social violation, was larger for other-owned objects in the PPS. These findings reflect that spatial proximity is considered in low-level perceptual processing, where near objects are automatically processed faster, and that ownership information exerts its influence at later post-perceptual stages.

Finally, in chapter 7, we investigated the neural activations associated with the interplay between space and ownership. Participants underwent fMRI scanning while performing an adapted version of the reachability judgement task. When participants judged reachable objects in the PPS, bilateral activations were observed in the parietal cortex, especially around the anterior portion of the intraparietal sulcus (aIPS). In the PPS, these regions were particularly engaged when judging the reachability of self-owned objects compared to other-owned objects. By contrast, objects in the EPS elicited more activation in medial prefrontal regions known to be associated with social cognition, eventually in relation to the presence of the virtual character. Going further, multivariate pattern analysis (MVPA) analysis revealed that activity in the ventral portion of the medial prefrontal cortex (mPFC) was specifically encoding self-owned objects in the PPS, whereas activity in the dorsal part of the mPFC was specifically tracking self-owned objects in both the

### 8.2.1. Behavioral signature of the interplay between space and ownership

PPS and EPS. These results suggest that estimating the reachability of objects depends on areas tuned to encode both the body's action capabilities in space, and self- and socially-relevant information: the parietal areas may signal the possible actions, and the mPFC may signal which objects are relevant for the self and thus available for action.

### 8.2. Synthesis of findings

Overall, the purpose of this thesis was twofold: (i) to determine whether object ownership and spatial location (i.e., PPS vs. EPS) interact during objects processing, and (ii), to identify the temporal and neural mechanisms underlying such interaction. Across a series of complementary studies, we adopted a multimethod approach combining behavioral measures, EMG, EEG, and fMRI, which provided converging evidence that ownership effects are not uniformly distributed across space, but are instead selectively expressed in the PPS (or, in other words, in the space dedicated to direct physical interaction with the environment).

# 8.2.1. Behavioral signature of the interplay between space and ownership

At the behavioral level, in chapter 4, we demonstrated the interaction between space and ownership through response time and reachability threshold, which served as a proxy to estimate the boundary of PPS representation. Responses were faster for self-owned objects, but only if these were located in the PPS. In addition, reachability thresholds were more distant for self-owned compared to other-owned objects. Altogether, these results could reflect a form of enhanced decisional efficiency, maybe due to more accessible action plans in this specific context.

The facilitation driven by self-owned objects appeared grounded in motor decision processes, as it was restricted to the actionable space. We hypothesized that object-oriented action regulation mechanisms, in particular those involving executive inhibition, particularly reflect this

### 8.2. Synthesis of findings

processing enhancement, considering its role in the monitoring of efficient action (Ridderinkhof et al., 2011). To test this hypothesis, we examined the efficacy of motor inhibition, as indexed by the rate and timing of partial errors (i.e., the number of initiated errors that were inhibited on time to end up on a correct response). The results revealed that initiated errors were corrected more rapidly and more frequently for self-owned objects in the PPS, which revealed more efficient monitoring of action plans in this condition. Interestingly, although the number of errors initiated was higher in the incongruent spatial configuration (i.e., other-owned objects in the participant's PPS), this ownership-related effect appeared only after a certain delay, which argues against an early, automatic bias that would have been indicative of a kind of impulsivity or automatic triggering of a specific response.

Altogether, these findings motivated a deeper investigation of the temporal and neural correlates underlying this interaction, as we aimed to determine when and where in the processing stream these factors interacted. The following sections address these questions to clarify the functional implications of the interplay between space and ownership in object processing for goal-directed action.

# 8.2.2. Temporal dynamics of the integration of space and ownership

When considered as a whole, our findings suggest that the temporal course of the interaction of space and ownership can be organized across different stages of neural processing. Indeed, we did not observe that it emerged at a single moment in time, but it rather seems that different information was integrated in a cascading manner.

# Stage I

#### 8.2.2. Temporal dynamics of the integration of space and ownership

In Chapter 6, we showed that global spatial information is processed at early perceptual stages. This was evidenced by the modulation of early ERP components, such as the N1 and the anterior N2, which responded respectively faster and stronger to objects located in PPS, but that were not influenced by ownership. The N1 component is typically associated with early attentional processes in the visual modality (Heinze et al., 1994; Hillyard et al., 1998; Johannes et al., 1995; Mangun, 1995), and the anterior N2 is associated with, in paradigm integrating goal-directed actions, an early inhibition of prepotent motor response (Liu et al., 2023; Mustile et al., 2021; Orlandi & Proverbio, 2019). This early enhancement likely supports perceptual prioritization and the preparation of potential actions, in order to facilitate quick responses to nearby stimuli (whether for defence or interaction). These results thus suggest that the brain rapidly detects and categorizes objects as "near" or "far" before evaluating their social or personal relevance.

# Stage II

Beginning between 250 and 300 ms post-stimulus onset, ownership-related information begins to shape object processing. In Chapter 5, we observed that, from this latency onward, errors were more likely to be initiated in incongruent spatial contexts (for instance, responding "not reachable" when an other-owned cup was located near the participant). Simultaneously, the P3 component emerged, and showed a larger amplitude for self-owned than for other-owned objects in PPS, which was interpreted as an increased motivational saliency when self-owned objects were actionable. At this stage, our brain appears to evaluate whether a given object is relevant for action not only based on its spatial location, but on whether it is situated in a space that affords a particular action *and* belongs to the self (or, to a larger extent, if it is relevant for oneself). This stage reflects a transition from a perceptual enhancement of near stimuli to a value-based prioritization, where self-relevant stimuli at hand receive preferential processing not because they are simply detected

### 8.2. Synthesis of findings

more easily, but because they are estimated as more valuable for behavioral interaction - in other words, more motivationally salient.

# Stage III

This latter stage of processing is characterized by contextual integration and social evaluation. In chapter 6 we observed that the anterior N400 component was found to be enhanced for other-owned objects in the PPS compared to in the EPS. The N400 is traditionally linked to semantic incongruity (Huang et al., 2014; Luo et al., 2013) and, in this context, it likely reflects the social mismatch of seeing others' objects in our near space. This suggests that the cognitive system not only encodes ownership and proximity, but also monitors violations of contextual expectations, including implicit social norms. Indirect additional evidence supporting a temporal distinction across processing stages comes from the analysis of partial errors: we observed an enhanced correction rate for self-owned objects in the PPS, whereas no ownership-related modulation was observed in the EPS. Given that corrections must occur within a narrow temporal window, it is likely that these corrections took place prior to the third stage of processing.

Although presented as a sequence, these three stages are unlikely to operate in a purely serial manner, but are more likely to operate in overlapping time windows. In particular, if the first stage appears too early to be really flexible, processes occurring at stage II and stage III likely influence each other and co-occur in decisional tasks requiring complex social inference, such as those involving other persons or ambiguous objects' location or characteristics. It is thus possible that the integration of spatial and social information is not straightforward, but is instead updated continuously. This proposition also suggests that PPS-related facilitation may not result from a unitary mechanism, but rather from the contribution of multiple partially independent processes operating on different timescales. On the one hand, there appears to be a rapid and proximity-based

enhancement in neural processing. This rapid process may have originally served a defensive function which has certainly been extended and adapted for intentional purposes (de Vignemont & Farnè, 2024). On the other hand, when the task requires it, slower mechanisms occur to finetune action preparation. At this stage, when required by the context, an additional ownershipsensitive mechanism may emerge, which integrates additional variables (such as motivational and social variables) to modulate and optimize action selection. This interpretation is in line with the fact that we observed an early effect of space location in chapter 6, but that, in the preliminary study of Chapter 5, we observed that processing information about ownership was faster than performing a reachability judgement. One can thus imagine that low-level spatial information, such as distance from the body, is processed rapidly; that high-level contextual information, such as ownership is processed at a later stage; and that computing the possible actions requires additional time to combine this information in order to build and select the correct movement. This interactive temporal cascade is consistent with Cisek's affordance competition hypothesis (2007) as reused by Bufacchi and Iannetti (2018), which posits that multiple potential action plans are simultaneously specified and maintained, with selection governed by both sensorimotor constraints and higher-order evaluative factors (e.g., value, social context). This framework will be explored further in section 8.3.2.

# 8.2.3. Brain mechanisms supporting the effects of ownership in peripersonal space

To complement the understanding gained from temporal analyses, we investigated the neural circuits involved in the interplay between space and ownership. In chapter 7, we observed that objects in PPS elicited bilateral parietal activations around the aIPS, consistent with the literature (Basile et al., 2024; Cléry et al., 2015; Grivaz et al., 2017). This activation was more extensive for self-owned objects, which was confirmed by region-of-interest analysis restricted to

the PPS core network. To our knowledge, this is the first demonstration that, during objects processing for goal-directed action, parietal activations reflect sensitivity not only to the possibilities of physical interaction with objects, but also to conceptual factors such as ownership.

The PPC (including the IPS) plays a central role in motor-related process, such as motor preparation, through the integration of multisensory information and the integration of spatial information in different frame-of-references. For instance, it subtends the integration of multiple sensory information in retinal and body-centred coordinates (Andersen & Buneo, 2002; Buneo & al., 2002), and contributes to the integration of visual and proprioceptive information to subtend adapted actions in space (Bernasconi et al., 2018; Filimon et al., 2009). Overall, these parietal activations are known to be involved in the processing of spatial relationship between items, and in computing object's location in the world relative to the body for goal-directed action, especially in the right hemisphere (Bartolo et al., 2014b; Basile et al., 2024; Rousseaux et al., 2014). Beyond replicating the parietal activations commonly reported in fMRI studies about PPS, the preferential engagement of parietal regions for objects located within the PPS provides additional evidences that reachability-judgement paradigms rely on action-relevant representations relative to the body.

When looking for areas preferentially coding for self-owned (vs. other-owned) objects in the PPS, we found greater activation in the anterior part of the IPL, which is recruited for goal-directed actions such as visually guided grasping or object use, especially in the left hemisphere (Van Elk, 2014; Zhang & Li, 2014), and regions around the IPS, involved in the sensorimotor transformation of spatial information required in reaching and grasping activities, especially in the right hemisphere (Andersen, 1995; Orban et al., 2021; Snyder et al., 1998; Rolls, 2020; Tanabe et al., 2005; Zhang & Li, 2014). Overall, our results suggest that, in contrast to other-owned objects (which may be subject to inhibitory influences attenuating their action-related encoding), self-

owned objects may facilitate the processing of objects for action by engaging a more relevant and therefore more robust representation of one's physical interaction with them. This would shape the sensorimotor encoding of objects for physical interaction by enhancing their consideration as action targets, which would be particularly relevant for adaptive behaviour in social context.

Besides, when exploring the EPS, we observed a partial mirror pattern: other-owned objects activated the right parietal cortex more than self-owned objects. Although this was not our primary interest, such activation is consistent with suggestions that the PPS network can simulate others' action potential in their own space, a function that may rely on mirror-like mechanism for action understanding and social coordination (Cardellicchio et al., 2013; Gallese et al., 2004; Rizzolatti & Rozzi, 2018).

To further understand how spatial location in turn modulated ownership processing, we analysed activity in the mPFC. Univariate analysis showed increased activation in the mPFC when objects were presented in the EPS compared to PPS, likely reflecting the heightened social salience of objects near the virtual character (Amodio & Frith, 2006). However, MVPA analysis revealed a different and more complex pattern: the vmPFC successfully classified self-owned objects among all conditions, but only in PPS. This aligns with proposals that the vmPFC encode affective value and motivational relevance in a context-dependent manner, rather than an absolute self-relatedness per se (D'Argembeau, 2013; Lockwood et al., 2018; Lieberman et al., 2019). Besides, dmPFC showed above-chance classification of self-owned objects across both the PPS and the EPS. This broader encoding may reflect the role of the dmPFC in maintaining self-other distinction (D'Argembeau et al., 2007; Verhagen et al., 2021) and in tracking socially relevant information for oneself in order to ensure smooth social interaction (Apps & Ramnani, 2017; Su et al., 2025;

### 8.3. Situating findings within theoretical models

Toelch et al., 2018). This includes, in the present case, monitoring whose objects one has the right to act upon, regardless of action possibilities.

Overall, these results support the view that the processing of self-owned objects is context-dependent, and relies on the coordinated involvement of multiple brain regions. In this account, the parietal cortex integrates spatial and ownership information for action preparation, possibly in coordination with neural mechanisms occurring in the mPFC to encode the social and motivational dimensions of objects in the environment.

### 8.3. SITUATING FINDINGS WITHIN THEORETICAL MODELS

To provide a comprehensive understanding of how ownership-related processes may modulate or interact with processing of objects in the PPS, it is essential to contextualize the above findings within the framework of existing theoretical models that address either ownership or PPS. Comparing these models is particularly interesting given that these constructs have emerged from different research traditions: whereas most PPS models are grounded in embodied cognition perspectives, models of object ownership primarily derive from the literature of self-relevance, which has strong ties to attentional processes and self-referential cognition. As mentioned in the introduction, our work primarily aligns with the embodied perspective of PPS, specifically with the integrative model proposed by Bufacchi and Iannetti (2018), which integrates Cisek's (2007) model to characterize stimuli processing in PPS (see below). At the same time, given that object ownership has been mostly studied within the self-relevance framework, we will also consider mainstream models in this domain, notably the Self-Attention Network (SAN, Humphreys & Sui, 2015) and an extension of this model accounting for mechanisms specific to object processing, the Self as Ownership in Attentional Prioritization (SOAP, Truong & Todd, 2017).

# 8.3.1. Object ownership in attention-based frameworks

To frame the role of ownership in self-relevant processing, it is important to consider models that have specifically addressed how the self modulates perception. In this context, the SAN constitutes the most well-spread framework in the literature. In their model, Humphreys & Sui (2015) proposes that self-related stimuli such as one's name, face, or personal belongings recruit specialized attentional networks that interact with general attentional systems. According to this model, self-relevant information enhances stimuli salience via the co-involvement of automatic bottom-up and of top-down mechanisms. Inspired by this approach, Truong and Todd (2017) developed the SOAP model, extending the SAN to encompass the specific case of object ownership. The SOAP framework thus conceptualizes ownership as a particular domain of self-relevance, and proposes that the attentional<sup>2</sup> saliency of owned objects is enhanced through two complementary mechanisms: (1) objects we own are processed as extension of oneself ("self-as-

I refer to them here with caution: while the SAN and the SOAP have become influential in the literature on self-prioritization, they are not fully aligned with the embodied, action-oriented framework underpinning the present thesis. In particular, I am conscious of the extended use of the term *attention* in the literature, a concern highlighted by Hommel et al. (2019) who argued that attention often functions as an umbrella denomination for heterogeneous

<sup>2</sup> Although these models offer an interesting and widely used account for understanding ownership effects,

mechanisms. For this reason, and to stay consistent with my theoretical stance while aligning with the propositions

made in these models, I use the term *attentional* mainly to refer to early-stage of information processing, such as

alerting and orienting (Posner & Petersen, 1990), while considering that later-stage processes are reflective of

mechanisms that may not solely fit with the concept of attention.

object"), just like for any self-related information, and more specifically, (2) ownership toward manipulable objects confers a sense of permission to act upon those objects ("self-as-subject").

Our empirical findings provide a nuanced test of the SAN and SOAP frameworks. In particular, our temporal analysis of the interaction between spatial location and object ownership reveals that early electrophysiological components such as the N1 and the anterior N2 were robustly modulated by spatial proximity, but not by ownership. Indeed, no significant modulation of the N1 component was observed as a function of ownership, despite the fact that early N1 effects have been taken as evidence for attentional capture by self-related stimuli in the SAN literature (Sui et al., 2012; Humphreys & Sui, 2015; Sui & Rotshtein, 2019). Following SAN terms, this suggests that early attentional effects driven by self-relevant objects were absent in our experimental conditions, and that early perceptual engagement appeared to be primarily driven by spatial location. Ownership thus did not automatically confer attentional salience in the early stages of perceptual encoding, contrary to the proposition of the SAN and to the self-as-object component of the SOAP. In contrast, in behavioral measures encompassing later stages of processing, measures were modulated by object ownership, indicating that self-relevant information influenced processing only after the object had been perceptually encoded and spatially localized. These post-perceptual modulations align with the idea that ownership is integrated as a high-level contextual variable. Such effects are better explained by contextual and goal-based frameworks, rather than by early attentional salience. They also align with recent findings that self-prioritization is not automatic, but contingent on task demands and on goal relevance (Golubickis & Macrae, 2023).

From a neurocognitive perspective, the contextual variations of self-prioritization for self-owned objects is mirrored in the functional role of the vmPFC: while the SAN/SOAP literature

depicts it as a dedicated, central and necessary node for self-referential processing, a growing body of evidence (e.g., Lockwood et al., 2018; Schäfer & Frings, 2018; Su et al., 2025; see Lieberman et al., 2019, for a review of the functional role of the mPFC) contradicts this view, and rather situates this region within circuits involved in subjective value computation, and, along with the dmPFC, in social relevance and goal-based decision making. Accordingly, vmPFC may not signal self-relatedness *per se*, but rather particular self-relevance information aligning with affective, social, or incentive relevance of external stimuli.

As a whole, these observations raise questions about the generalizability of the SAN and SOAP accounts: while the *self-as-object route* may explain ownership and self-relevance biases in paradigms requiring participants to evaluate self-related aspects explicitly, such as shape-label tasks, association tasks, or classification tasks, our findings suggest that these effects are not robust in action-oriented tasks. Regarding the *self-as-subject route*, it may contribute to the non-uniform pattern observed across space, as it considers attentional benefits of self-ownership depending upon availability for action. However, it is unlikely that the observed effects in the present thesis are due to a specific bias in "attentional tuning", as proposed by Truong and Todd (2017). In our results, we found no evidence of an effect of ownership on early attention allocation. The intentional restriction of the SOAP model to attentional salience may thus be insufficient to account for the results that we previously reported. Extending the self-as-subject route may however offer an interesting approach for interpretation; in this regard, the authors themselves point to a possible direction by mentioning the requirement for embodied and enactive accounts of self-prioritization for objects.

# 8.3.2. An embodied account of ownership relevance for action

Turning to embodied theories, the interactive behaviour framework proposed by Cisek (2007; Cisek & Kalaska, 2010), posits that multiple competing actions are being prepared in parallel at all times. Action is not initiated in a serial way, but emerges through competition between contextually appropriate motor plans. Bufacchi and Iannetti (2018) enriched this framework by incorporating the concept of PPS, and included this approach in their model: they proposed that PPS comprises multiple overlapping and graded sub-fields, each tuned to specific behavioral or motor functions. The relevance of potential contact-based actions, whether prospective or defensive, is computed in these sub-fields. This contact-based theorization explains why objects closer to the body benefit from a processing advantage: the relevance of the entire set of potential actions increases with proximity to the body. In term of relevance, we may imagine a similar mechanism regarding ownership: self-owned objects may engage a richer or more strongly activated set of potential actions, which in turn facilitates motor-related processes such as faster response initiation and more efficient action control.

Crucially, Cisek proposes that neural processing of items in the environments unfolds in two stages: an early specification stage that specifies and represents the multiple potential actions in parallel, and a later stage of biasing influences that filters the possibilities and selects one action for execution. Our temporal dissociation between early spatial effects and later ownership effects fits this dual-stage organization precisely. Early effects, such as the modulation of the N1 and the N2, may reflect processes involved in the early specification stage. Nearby objects, regardless of their ownership, are encoded as potential targets for multiple actions. The latter stages described in the temporal dynamics presented in the section 8.2.2 may thus correspond to the biasing

processes, in which the system incorporates higher-order variables<sup>3</sup> (ownership, social norms, affective and motivational value, *etc.*) to resolve competition among action possibilities. Ownership may thus operate by weighting the value of individual action possibilities (*affordances*), making self-owned objects more likely to win the competition for action. This would also explain the difference in activation in parietal areas between self- and other-owned objects in the PPS: action possibilities toward other-owned objects may be more filtered than those toward self-owned objects, leading to weaker activations. Such interpretation aligns with the role of the PPC in the representation and discrimination of action specificity (Urgen & Orban, 2021; Orban et al., 2021), and in its contribution to the integration of higher-order information such as conceptual, semantic, or social information in action-related processes (Fornia et al., 2024; Hawellek et al., 2016; Xu, 2018; Yamazaki et al., 2009). Neuroimaging studies reporting vmPFC and dmPFC activations for self-owned and other-owned objects (Lockwood et al.,2018; Lenglart et al., In prep; Turk et al., 2011) may therefore illustrates these high-level bias inputs into the second wave, enhancing the weight of action possibility toward ownership-relevant objects.

One may ask, however, how the above-mentioned model may align with our results; indeed, how the expected response (e.g., pressing a button) may be affected by different action possibilities? In this interactive behavioral approach, the sensorimotor system encodes partial action plans through distributed neural mechanisms, each tuned to particular stages of action specification. In other words, any action relies to a greater or lesser extent on shared parts of networks recruited for the preparation of other competing actions (Cisek et al., 2010). Accordingly,

<sup>&</sup>lt;sup>3</sup> Falling under the larger term of *cognitive information* used by Cisek.

the more the task shares common parameters with the multiple prepared actions, the more the final response will reflect these activations: for instance, estimating the reachability of a cup could share more parameters with prepared actions toward this cup than judging its color. Bufacchi and Iannetti (2018) added that only part of the available information is processed at the different stages of neural computation, as "neurons and networks underlying PPS measures are unlikely to have access to perfect situational information" (p. 1087), and that these specific neural responses constitute only a step to the ultimate selection of action. Thus, early responses will almost exclusively rely on early stages of processing and integrate fewer high-level information. This graded perspective of competing action sharing common motor components may account for the temporal distinction observed in our results. Moreover, Cisek's model takes a distributed-control perspective of executive control of motor output, by postulating that control processes occur within the same sensorimotor circuits responsible for executing actions rather than relying on an external "inhibitory module", (Eisenreich, 2017; Pezzulo & Cisek, 2016). The integration of this distributed-control perspective may explain why, in Chapter 5, more efficient inhibitory control was observed for self-owned objects in the PPS (an effect consistent with the earlier and enhanced neural response observed in Chapter 6). In situations involving time pressure or limited processing capacity, the system may have time to process (and thus prioritize) only the most behaviourally relevant information, such as self-relevant information located near the body.

# 8.3.3. Toward a contextualized model of action fields in PPS

Our results encourage a theoretical extension of the action-field model of PPS of Bufacchi and Iannetti (2018), not by challenging its foundational claims, but by elaborating further how high-level conceptual and social variables, such as ownership, modulate action selection. In this framework, ownership does not redefine the spatial structure of PPS, but instead modulates the

competitive weighting of action possibilities associated with stimuli encoded, ultimately reflecting the relevance of action toward the self- or other-owned object (Figure 32.a.). This modulation is context-dependent rather than immune to contextual influence: it emerges when ownership is behaviourally meaningful and when goal-directed action selection mechanisms are engaged. I propose that such influences are implemented during the biasing wave described in Cisek's affordance competition model, after the brain has specified the set of potential actions (Figure 32.b.). Importantly, this proposition does not imply a distinct "ownership field" within the PPS, but reflects the reconfiguration of existing actions fields based on the relevance of ownership. In this respect, just like Fujii et al. (2007) showed that, in non-human primates, parietal neurons encoding actions possibilities stopped responding when those objects were simultaneously accessible to a dominant conspecific, it is possible that activity within the fronto-parietal network supporting the processing of objects in the PPS may be modulated (and, particularly, inhibited) when objects are socially unavailable for action. This perspective not only explains our own findings, but also accounts for the results of Patané et al. (2021), who observed enhanced multisensory facilitation in PPS for self-owned objects. Within the present framework, these effects may reflect a context-dependent expansion of PPS neurons' receptive fields.

To a larger extent, we may hypothesize that PPS is composed of value-sensitive fields sensitive to the behavioral significance of stimuli. This includes not only socially significant stimuli, such as those owned by the self or by others, but also inherently valuable ones, as shown by Gigliotti et al. (2021), which demonstrated that reward value modulates the extent of PPS representation and how one exploits it. In short, a value-based weight attributed to stimuli (whether social or motivational) may reshape the spatial profile of the action fields within PPS and selectively enhance or decrease their activation.

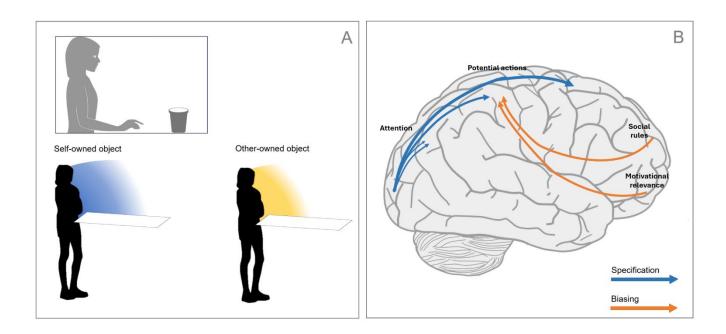


Figure 32. (A) Schematic representation of PPS as the sum of a set of fields reflecting the relevance of actions. When considering self-owned (blue) compared to other-owned (yellow) objects, the PPS extent increased, as the action's fields aiming at creating contact are more relevant. (B) Social rules, such as the tracking of self-owned (i.e., authorized) objects, guide interaction by modulating the selection of most relevant targets. Spatial information contributes to the specification of potential actions through an early attentional filter, allowing actions that are physically possible and most relevant for rapid interaction (i.e., toward targets in the PPS). Higher-order information, such as ownership status, exerts its influence during the biasing wave. For clarity, the diagram illustrates this mechanism through two distinct components in the vmPFC and dmPFC; however, the mPFC likely operates as a more functionally heterogeneous structure, with multiple subregions and neuronal populations encoding a range of social and contextual information. The vmPFC and dmPFC are thus likely to influence each other during social decision-making, which is corroborated by their dense reciprocal connections.

# 8.3.4. The role of ownership and interpersonal distance in preventing social intrusion

Given the explanations proposed above, the pattern observed in our results may mainly emerge in contexts where the owner of the other-owned objects does not represent a threat, such that approach-related actions remain more relevant than withholding action. In such contexts, ownership may bias action selection primarily based on the behavioral relevance of available objects. However, it remains unclear whether this pattern would persist in threatening social contexts. For instance, if the confederate appears angry or aggressive, other-owned objects might become more behaviourally relevant by affording defensive action. Alternatively, in the same context, social norms and the need to avoid conflict might instead accentuate the ownership effects, completely suppressing the engagement toward other-owned objects.

This line of reasoning highlights the functional heterogeneity of the PPS, and its differential role in different relevant actions. In this regard, it is important to note that, as depicted in Figure 32.a., ownership-based modulations of PPS are unlikely to affect the entire peripersonal space in a uniform manner, and to suppress the relevance of any contact-based interaction. The zone closest to the body, sometimes referred to as *personal space* (the space in which social intrusion is perceived as uncomfortable), remains highly sensitive to potential contact, even for other-owned objects. Indeed, when someone places a personal item, such as a phone or a cup, too close to our body, it is common to experience a form of discomfort or intrusion. Such reactions suggest that objects in this personal space retain strong sensorimotor (and potentially social) relevance, possibly linked to a defensive and protective function in a social context. Even though it remains untested in the present thesis, in this area of space, the weight of higher-order information such as ownership may change. Instead, the weight of any cue indicating a potential threat or any negative

valence may be heightened, and the contact-based computation may be more governed by fundamental proximity and movement-based mechanisms for body protection.

These considerations resonate with the theoretical model of Coello and Cartaud (2021) which proposes that interpersonal distance (IPD) is constructed upon the sensorimotor basis of PPS to maintain physiological homeostasis by preventing intrusion. From this perspective, IPD represents a socially shaped extension of PPS. In the present case, one faces a specific social configuration in which the social dimension is not (or, at least, not solely) carried by the presence of another person, but by their symbolic extension: their personal objects. It is therefore plausible that ownership-based modulation follows a spatial gradient anchored in PPS mechanisms: the innermost area (the personal space) functions as a "no-go" zone for other-owned objects, similar to other persons. Beyond the personal space, a more flexible space may emerge where action relevance is determined by task demands and contextual information. This division reflects recent findings by Geers and Coello (2023), who reported correlations between personal space, PPS representation, and IPD preferences. The authors proposed that the sensorimotor properties of PPS, especially the more defensive-oriented properties at stake in the personal space, serve as a spatial reference to specify the appropriate IPD, which modulates perceptual processes such as multisensory integration. This interpretation opens avenues for future research: for instance, it would be interesting to examine physiological markers such as electrodermal activity to index bodily arousal or discomfort in response to other-owned objects placed at different locations within PPS (notably when comparing its innermost region compared to its boundary).

In line with the mutual respect of IPD that underlies social interactions, Ariga (2016) reported that individuals tend to place their own belongings at a greater distance from other's items, suggesting that the psychological boundaries of the personal space may extend to the space

surrounding one's belongings, creating a "transposed personal space". This means that owning an object may create an implicit buffer zone around it. Such a buffer may prime interactants to respect a larger interpersonal distance when an object is placed near its owner. This observation invites further investigation: for instance, can the presence of owned objects around the body modulate IPD, as measured behaviourally or physiologically? More broadly, the use of ownership as a spatial social marker may also indicate that ownership can be used as the marker of one's "territory". Like many species mark and defend specific zones, where intrusion may provoke defensive behaviour, humans may use objects placement to delineate a form of social territory and indicate to others where they can or cannot go. Behaviours such as placing photographs on a desk or a bag on a seat in a train can be seen as subtle territorial claims to discourage intrusion. These behaviours raise questions about how these territories, or transposed personal spaces, are respected, and how individuals react to their invasion. Beyond comfort-related concerns, the invasion of personal space has been shown to induce both short- and long-term impairments, such as psychological distress and the development of pathological behaviours (Calhoun, 1962). It remains to be determined whether similar consequences arise from the intrusion into extended personal space. Overall, future research could directly compare responses to invasion of personal space (i.e., near the body) and transposed personal space (i.e., near an owned object), the interactions between these two representations of space, and how persons spontaneously respect such symbolic markers of a territory.

### 8.4. LIMITATIONS AND THEORETICAL AND EMPIRICAL PERSPECTIVES

The discussion so far highlights that the way we perceive and prepare actions toward objects depends on both where they are in relation to the body and who they belong to. These findings revealed how subtle changes in context, including parameters such as social setting or personal

meaning, may reshape the processing of objects for action. While clarifying when and where ownership shapes object processing in the PPS, this thesis rests on theoretical and methodological commitments that leave open the question of whether similar processes adapt outside the laboratory, across different daily life situations.

# 8.4.1. From situational to personal: a graded representation of ownership significance

In the present thesis, a central objective was to isolate the cognitive and neural processing of ownership *per se*, and disentangle it from its numerous semantic and affective associations. As underlined in prior work (e.g., Morewedge, 2021), ownership is a multifaceted construct that is often encountered in conjunction with various dimensions (including, but not restricted to, legal status, personal identity, affective bond, or autobiographical memory). To identify the core mechanisms of ownership-related modulation, we adopted a deliberately minimalistic approach and operationalized ownership as an elementary and controlled status, which was necessary to delineate the foundational processes by which ownership influences perception and action.

Interestingly, this experimental simplification may explain why the effects we observed primarily reflected ownership as a social mediator, in terms of behavioral and contextual appropriateness. Indeed, object ownership may in essence not mark an emotional or mnemonic bond with an object, but constitute a situational marker to guide interaction. For instance, in everyday contexts, such as dining in a restaurant, ownership distinctions (e.g., which glass of water belongs to whom) are respected not necessarily because of emotional attachment to the glass, but because such distinction enforces the social norm of not drinking from someone else's glass. When considering common domestic scenarios, this idea of a *situational ownership* may even be pushed toward a temporary or context-dependent characteristic: considering a shared household where two individuals use the same set of dishes. Although ownership of the dishes may be collective as

a whole, different situations may impose transient ownership distinction. If one person prepares two cups of coffee, each cup is implicitly assigned to a specific person, and crossing this boundary (e.g., drinking from both cups without distinction) may elicit protest. These examples illustrate that ownership is not necessarily absolute or permanent, but, in every life, may be flexible and transient although necessary. In this sense, tracking ownership may serve as a mediator of social coordination, even in the absence of strong emotional attachment.

Accordingly, while isolating mere ownership allowed us to identify its role as a social cue, real-life situations may involve richer ownership bounds that carry significant personal meaning. It would be interesting, in future studies, to manipulate the personal characteristics of objects to determine how these dimensions modulate ownership-related effects. For instance, highly self-related or emotionally-charged items might elicit more pronounced behavioral modulations than items carrying low social value. From this perspective, it is also worth considering cultural variability: if tracking ownership serves for both personal identity and respect of social norms, its behavioral impact may vary across cultural contexts. In societies where private property is considered negatively and where communal sharing is the norm, like in traditional kibbutz or in hunter-gatherer societies (Mayor, 2012; Ruffle, 2002), the cognitive weight assigned to ownership as a mediator of social coordination may be diminished or abolished. Cross-cultural studies would therefore be valuable in understanding the universality of such effects.

# 8.4.2. Others' presence and the social encoding of ownership

Following the proposition that ownership embodies a central social dimension, we observed that effects emerging in the EPS (that is, in the vicinity of the virtual character) were not consistently present across all studies. Specifically, no significant ownership-related modulation of RTs for stimuli in EPS was found in Chapter 4 or through visual inspection of the data of the

preliminary online study presented in Chapter 5. This absence of modulation is unlikely to be explained by difficulties in perceiving the color (and thus ownership) of the stimuli presented at the farthest distances as, in the preliminary study of Chapter 5, the RTs for ownership identification remained constant across all distances. The fact that RTs did not increase in the EPS suggests that participants did not experience greater difficulty in identifying ownership. In contrast, the following experiments revealed a mirror-like pattern in RTs, whereby the behavioral facilitation observed for self-owned objects in PPS was echoed for other-owned objects in EPS. This mirror pattern of results was further supported by our fMRI findings, which showed increased parietal activations when other-owned objects were presented in the EPS. Interestingly, we also observed the emergence of an anterior N400 in Chapter 6 for other-owned objects in the PPS, which we interpreted as a social or normative incongruence. A coherent interpretation of these observations relies on the social presence of the character in the virtual environment: in early versions of the paradigm, such as in the study reported in Chapter 4 and the preliminary study of Chapter 5, the virtual character was minimally realistic, as it was represented as a static image. In the later studies, the virtual character was animated (breathing and blinking), and participants were introduced to a brief visual scene at the beginning of the experiment where the other-owned objects were assigned to the character, whereas in the first studies it was established via a short verbal or written instruction.

This shift in vividness may explain why mirror-like ownership effects emerged only in later versions of the paradigm. Importantly, this view is in line with findings from Constable et al. (2014) who showed that the presence of the object's owner was a condition for observing some, but not all, biases associated with ownership. It is plausible that the social presence of an agent is required for ownership to be fully encoded as a constraint influencing decision and action, an

interpretation that strengthens the role of ownership in social interaction. The present thesis did not directly compare the presence and absence of the confederate nor of the realism of the virtual character on ownership-related effects, which could constitute an interesting research line. To test this hypothesis directly, future research would compare ownership effects in the presence and absence of a virtual character, or examine how the realism and the presence of human-like characteristics of a virtual character may affect the observed effects. These variations could be complemented by including measures or questionnaires of virtual co-presence, to directly correlate how "social" the situation was perceived, and how it impacted the respect for other's property.

In addition, all experiments in the present thesis were conducted in a virtual environment. While it was demonstrated that manipulation of space (Bartolo et al., 2014) and ownership (Lockwood et al., 2018) elicit cerebral activations comparable to those in real-life settings, it is possible that the processing of the social value of objects and, to a larger extend, of the context was diminished compared to a situation involving a real human confederate. Thus, comparing the effects of ownership in virtual and real-life contexts constitutes an interesting perspective.

# 8.4.3. Facilitative and inhibitory accounts of ownership-related effects

Finally, whether the influences of ownership are facilitative (i.e., an enhancement of self-owned objects) or inhibitory (i.e., an inhibition of other-owned objects) remains unanswered. Given the inherently social role of objects ownership, it is difficult to disentangle these two possibilities in an experimental context. As previously discussed, (see p. 30 of the present thesis), including a condition with a neutral, ownerless object is problematic. In our current societies, encountering truly unowned objects is highly uncommon, and such stimuli are likely to be interpreted inconsistently across participants, which would introduce substantial inter-individual variability in perceived ownership attribution.

#### 8.4. Limitations and Theoretical and empirical perspectives

The present thesis provides evidence that supports both facilitative and inhibitory interpretation, which suggest that, consistently with both social and self-relevant aspects of ownership, ownership may indeed exert both a facilitating and inhibiting influence on object's processing. For instance, in Chapter 5, the observed increase in executive inhibition for self-owned objects located in PPS, and in Chapter 6, the enhanced P300 amplitude under the same conditions, may be interpreted as evidence for a facilitative effect. Conversely, the greater N400 amplitudes elicited by other-owned objects in the PPS in Chapter 6 and the increased activation of the presupplementary motor area (pre-SMA) for other-owned objects in the PPS (compared to the EPS) in Chapter 7 may instead reflect an inhibitory response possibly associated with action suppression. In addition, previous authors, such as Constable et al. (2011) rather argued in favour of the inhibitory account, suggesting that "the action system is blind to the potential for action towards another person's property".

Although being beyond the scope of this thesis, in order to further investigate the presence of such inhibitory versus facilitatory mechanisms at the level of the motor system, we designed a TMS experiment where participants viewed self- and other-owned objects while single pulse was delivered over the primary motor cortex in order to probe corticospinal excitability as a direct index of action-related motor readiness. Preliminary findings (see Appendice 9.1) from this experiment suggests that other-owned objects in the PPS elicits reduced corticospinal excitability relative to when those same objects are presented in extrapersonal space, where their owner is present and socially entitled to interact with them. However, as these are preliminary results, they are to interpret with caution.

# 8.4.3. Facilitative and inhibitory accounts of ownership-related effects

Overall, future studies may thus try to explore further whether ownership modulates objects processing for goal-directed action through inhibiting or facilitating influences and, if both are observed, to delineate their respective effects.

#### 8.5. Conclusion

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Overall, this thesis paves the way for an extension of the current conceptualization of the PPS. Traditionally understood as a sensorimotor interface defined by bodily proximity and physical availability for action, the PPS (and the mechanisms occurring within its boundary) is shown to be sensitive not solely to spatial parameters, but also to abstract social constructs such as ownership. Here, ownership does not merely mark an abstract and unconditional personal relevance; it constitutes a contextual cue that modulates spatial representation and action selection, by pointing not only what is physically accessible, but also socially relevant. This work proposes thus that PPS may be better understood if considered as a socially structured action space, either when elaborated in a social context or if encompassing objects characterized by their social value. Accordingly, potential actions are weighted according to both sensorimotor constraints and normative social information.

In sum, the findings presented here call for models of perception and action that move beyond proximity-based frameworks and suggest that they should incorporate context-sensitive layers of processing in relation to social contexts. In this way, they add to the current debate about the different functions of the PPS. While rapid proximity-based processing may operate independently of higher-order features (e.g., in contact-based defensive responses), incentive or appetitive-oriented actions appear to engage slower mechanisms that integrate contextual characteristics in a larger body-centred space. To advance toward more ecologically valid models of PPS, future research would consider how sensorimotor functions are shaped by both the physical properties of the environment and the contextual (specifically, the social and normative) information in which everyday interactions are grounded.

# 9. References

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## 10. APPENDICES

#### 10.1. METHOD AND PRELIMINARY RESULTS OF THE TMS EXPERIMENT

Prior research suggests that the sensorimotor system is sensitive not only to spatial parameters, such as whether an object is located in the PPS, but also to the social parameters of the object. Constable et al. (2011) suggested that affordances associated with others' property may be inhibited (or not perceived) by the sensorimotor system. This view is supported by neuroimaging findings showing that activation of parietal areas involved in the perception of objects in the PPS for goal-directed action are modulated by ownership (Lenglart et al., in prep), and that processing other-owned objects in the EPS recruits the pre-SMA, an area often associated with motor inhibition. However, no direct evidence of such modulation is available.

To address this, we employed single-pulse transcranial magnetic stimulation (TMS) over the primary motor cortex (M1) to index the recruitment of motor circuits during the perception of graspable objects in PPS (Cardellicchio et al., 2011; 2013), while participants passively observed objects labelled as self- or other-owned presented in the PPS or in the EPS.

#### **METHOD**

#### **Participants**

Twenty-five right-handed participants with normal or corrected-to-normal vision, no history of epilepsy, no ferromagnetic implant, and no history of neurological or psychiatric disorders were recruited ( $M_{\rm age} = 23.64$  +/- 2.14; 14 females). All participants received an information letter one week before the experimentation, and gave written informed consent prior to participation. The experiment was approved by the local ethics committee (Ref. No. 2024-810-S131) and conducted in accordance with the Declaration of Helsinki (2013).

### Materials and procedure

Prior to the experimental condition, two real mugs were presented on a table. As ownership was cued by color, the two mugs were physically identical and differed only by their color (one blue, and one yellow). Participants were gifted one of the two mugs, and asked to store it with their belongings. The other mug was assigned to a virtual character, and both mugs were replicated in the virtual environment for the experimental part of the task.

In the experimental part of the task, participants were seated in a quiet experimental room in front of a 27" computer screen with a refresh rate of 120 Hz displaying a 3D virtual scene. The scene was developed using Unity software and consisted of a wooden table and a male virtual character with a neutral facial expression positioned at the far end of the table. The virtual character was selected from the ATHOS database (Cartaud & Coello, 2020). Participants were instructed to imagine themselves sitting at the virtual table from a first-person perspective.

Before the main experimental task, participants performed a brief ownership classification task to ensure that ownership was correctly memorized and to familiarize themselves with the experimental setup. During this task, for each trial, one of the two mugs was presented on the screen, and the participants were asked to classify it as either their own or belonging to the virtual character by pressing the "C" or "V" keys on a keyboard with their left hand. Each cup was classified 10 times, yielding a total of 20 trials. The entire familiarization phase lasted approximately 2 minutes.

To determine the location of M1 for stimulation during the experimental session, single-pulse TMS was applied using a figure-of-eight coil to elicit MEPs. The optimal scalp position ("hotspot") was identified for each participant by locating the site that produced maximum

amplitude in the right first dorsal interosseous (FDI) muscle. Pulse intensity was set at 120% of the resting motor threshold, defined as the minimum intensity eliciting MEPs of at least  $50\mu V$  in 50% of trials across a minimum of 10 trials. For the rest of the experimental session, EMG activity was recorded from two muscles of the right hand: the FDI, and the abductor digiti minimi (ADM). The FDI, known to be involved in precision pinch (such as holding the handle of a mug), served as the primary target muscle (supposed to be activated by the TMS), and the ADM, rather involved in power grasp, was used as a control site (supposed to be not activated by the TMS). EMG signals were recorded using a Delsys Trigno acquisition system (Delsys Inc., Boston, MA), with one of the two wireless electrodes placed on each muscle. To monitor the position of the coil relative to the hotspot on the participant's head, a custom system continuously displayed the positions of markers placed on both the head and the coil during the task.

At the beginning of the experiment, participants completed a baseline block of 20 trials. In this block, they were asked to fixate on a virtual environment in which the virtual character was present at the far end of the empty table, with no mug placed on it, while TMS pulses were sent 75 or 250 ms after stimulus onset, as in the main experimental task. The same baseline block was repeated at the end of the main task, as corticospinal excitability is likely to fluctuate over the duration of the task due to factors such as attention or tonic motor system activation. For each delay (75 ms and 250 ms), the maximum MEP amplitudes recorded across the baseline trials were averaged. The averaged values served as a baseline for normalizing the MEP amplitudes obtained during the experimental task.

In the main experimental task, each trial began with a visual mask (blurred visual scene with a fixation cross) lasting between 450 and 550 ms, followed by the virtual scene shown for 500ms (Figure A1). The virtual scene was composed of the virtual environment containing the

agent, and a single cup (either the participant's or the character's cup). The cup appeared at one of the six possible distances (either in the PPS at 10, 15, or 20 cm or in the EPS at 90, 95, or 100cm from the participant's position). A single TMS pulse was delivered either 75 ms or 250 ms after scene onset, to probe motor excitability at distinct processing stages. After stimulus offset, a second mask composed of an empty virtual scene was displayed for 4000ms to allow motor activity to return to baseline.

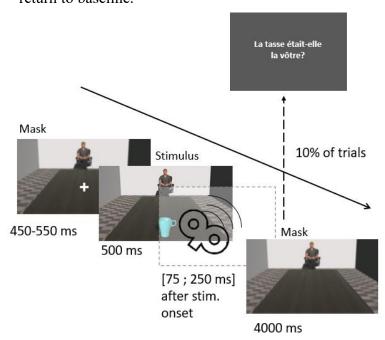


Figure A1. Illustration of the sequence of events within a typical trial during the main experimental task.

To ensure task engagement, in approximately 10% of trials (called filler trials), participants were asked to answer a question concerning either the ownership or the spatial location of the cup. These questions appear after stimulus presentation, and require a binary (yes/no) oral response.

# Statistical analysis

As the EMG data were recorded using wireless electrodes, no high-pass filtering was applied. The peak of each EMG burst was automatically detected as the maximum amplitude from baseline within a 70-ms time window following TMS stimulation, and subsequently recorded.

Offline processing of EMG signals was conducted using MATLAB version 2025.a (MathWorks Inc, 2025), and statistical analyses were performed using R version 4.4.2 (R Core Team, 2024). For statistical analyses, MEP peak amplitudes that deviated by more than two standard deviations from the individual mean within each condition were excluded, corresponding to 2.9% of trials. The remaining MEP values were then normalized by calculating the percentage change relative to baseline, which was determined by averaging the pre- and post-experiment baseline recordings.

Data were analysed using linear mixed models with Space (Peripersonal, Extrapersonal) and Ownership (Self-owned, Other-owned) as fixed effects, implemented via the lme4 (v1.1–35.3; Bates et al., 2015) and lmerTest packages (v3.1-3; Kuznetsova et al., 2017). The model took into account inter-individual differences by systematically including participants as a random effect. Given that coil-to-hotspot distance is a major source of variability in EMG amplitude, this distance (computed as the absolute distance between the coil marker and the position of the hotspot based on their respective x, y, z coordinates) was included both as a fixed effect and as a random slope to capture trial-level variability. The resulting model was specified as:

MEP Amplidude  $\sim$ Space \* Ownership + coil distance + (1 + coil distance | subject)

As the main objective of the study was to assess the Space  $\times$  Ownership interaction at two stimulation delays (TMS at 75 ms and at 250 ms post-stimulus onset), two identical models were constructed, one for each condition. When a significant interaction was observed, the effect of ownership in the PPS and in the EPS was further investigated via paired-samples t-tests using the pairs function of the package emmeans. For all analyses, the alpha level was set at .05.

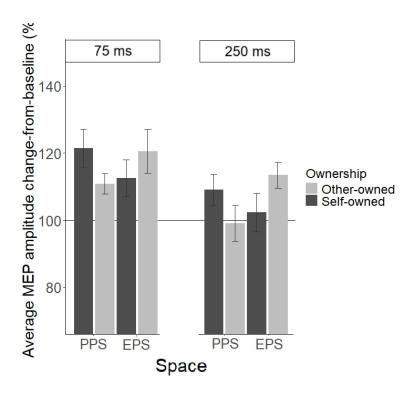


Figure A2. Average change in amplitude from baseline (%) as a function of Space and Ownership when stimulating M1 75 ms and 250 ms after stimulus onset. Error bars represent standard errors. The horizontal line represents the baseline.

As of the 1<sup>st</sup> of July 2024, 25 participants have been recruited. Among these, the data of two participants were not exploitable (one did not finish the experiment, and the other developed anticipation strategies and did not follow the instructions). Among the remaining 23 participants, the data of 19 participants have been successfully pre-processed, and the data of the remaining 4 participants need additional processing steps and could not be included in the preliminary analyses.

The LMM analysis on the amplitude of the MEPs revealed no main effect of Space (t (1493.75) = -1.32, p = 0.18) and no main effect of Ownership (t (1493.20) = -0.92, p = .36). A trend toward interaction between self and ownership was reported (t (1493.94) = 1.96, p = .052). However, no significant interaction survived correction during the pairwise t-tests (all p > .065, all p corrected > .25).

250 ms

The LMM analysis on the amplitude of the MEPs revealed a main effect of Space (t(1464.25)) = -2.75, p = .006), with larger amplitudes in EPS (M = 107.85, SD =20.00) than in PPS (M = 104.02, SD = 21.61), as well as a main effect of Ownership (t(1464.09)) = -2.31, p = .021), with smaller amplitudes for self-owned objects (M = 106.00, SD =21.06) compared to other-owned objects (M = 106.21, SD =20.20). An interaction between space and ownership was reported (t (1463.23) = 2.90, p = .004). Specifically, for other-owned objects, MEP amplitudes were smaller in the PPS (M = 99.02, SD =23.26) than in the EPS (M = 113.41, SD =16.76, t(1476) = -2.75, p = .006,  $p_{corrected}$  = .024) and, in the EPS, MEP amplitudes were smaller for self-owned compared (M = 102.29, SD =25.16) to other-owned cups (M = 113.41, SD =16.76, t(1476) = -2.31, p = .020,  $p_{corrected}$  = .041). No other significant interaction was reported (all p > .07, all  $p_{corrected}$  > .10).

DISCUSSION

Although consisting of only preliminary results, an interesting pattern appears to emerge from the data. Specifically, when single-pulse TMS was applied over M1 at 250 ms following the presentation of an owned cup on a virtual table, we observed that MEPs were reduced for other-owned objects when located in the PPS compared to in the EPS. Notably, this effect was not observed when stimulation was applied earlier, at 75 ms post-stimulus onset, although a pattern

seemed to appear at visual inspection. This temporal modulation of the effect of ownership is in line with our previous results (Lenglart et al., 2023, 2024), which suggests that mechanisms similar to those associated with behavioural performance may apply to motor excitability in M1.

It is also worth noting that, overall, we did not observe larger MEPs in the PPS than in the EPS. This result was expected as it is consistent with prior work by Cardellicchio et al. (2013), who proposed that the presence of another individual capable of acting upon objects in EPS may render that space socially actionable, thus abolishing the typical PPS advantage in motor excitability.

As a whole, these preliminary observations suggest that ownership may be embodied within the sensorimotor system, potentially through an inhibitory mechanism affecting motor responses to other-owned objects in the PPS, as suggested by Constable et al. (2011). This inhibition might reflect a form of socially modulated action suppression with reduced affordances when one object is reachable but not authorized to be acted upon due to social norms (i.e., in the participant's PPS), as compared to when located near its owner (i.e., in the participant's EPS). This interpretation is also in line with results of our fMRI studies (Lenglart et al., In prep.), where we observed an increased activation of the pre-SMA, a structure often associated with motor inhibition (Nachev et al., 2007, Obeso et al., 2013), when processing other-owned objects in the PPS compared to in the EPS. Nevertheless, given the preliminary nature of these findings and the need for more thorough data analysis, we need to interpret these results with caution.

#### 10.2. DESCRIPTION OF THE PREPROCESSING PROCEDURE USING FMRIPREP.

## Anatomical data preprocessing

A total of 1 T1-weighted (T1w) images were found within the input BIDS dataset. The T1w image was corrected for intensity non-uniformity (INU) with N4BiasFieldCorrection (Tustison et al. 2010), distributed with ANTs 2.5.0 (Avants et al. 2008, RRID:SCR 004757), and used as T1wreference throughout the workflow. The T1w-reference was then skull-stripped with a Nipype implementation of the antsBrainExtraction.sh workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and grey-matter (GM) was performed on the brain-extracted T1w using fast (FSL (version unknown), RRID:SCR 002823, Zhang, Brady, and Smith 2001). Brain surfaces were reconstructed using recon-all (FreeSurfer 7.3.2, RRID:SCR 001847, Dale, Fischl, and Sereno 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile ANTsderived and FreeSurfer-derived segmentations of the cortical grey-matter of Mindboggle (RRID:SCR 002438, Klein et al. 2017). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with antsRegistration (ANTs 2.5.0), using brain-extracted versions of both T1w reference and the T1w template. The following template was were selected for spatial normalization and accessed with TemplateFlow (23.1.0, Ciric et al. 2022): ICBM 152 Nonlinear Asymmetrical template version 2009c [Fonov et al. (2009), RRID:SCR 008796; TemplateFlow ID: MNI152NLin2009cAsym].

#### Functional data preprocessing

For each BOLD run found per subject, the following preprocessing was performed. First, a reference volume was generated, using a custom methodology of fMRIPrep, for use in head motion

correction. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using mcflirt (FSL, Jenkinson et al. 2002). The BOLD reference was then co-registered to the T1w reference using bbregister (FreeSurfer) which implements boundary-based registration (Greve and Fischl 2009). Co-registration was configured with six degrees of freedom. Several confounding time-series were calculated based on the preprocessed BOLD: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, Power et al. (2014)) and Jenkinson (relative root mean square displacement between affines, Jenkinson et al. (2002)). FD and DVARS are calculated for each functional run, both using their implementations in Nipype (following the definitions by Power et al. 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors was extracted to allow for component-based noise correction (CompCor, Behzadi et al. 2007). Principal components are estimated after high-pass filtering the preprocessed BOLD time-series (using a discrete cosine filter with 128s cut-off) for the two CompCor variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM, and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that instead of eroding the masks by 2 pixels on BOLD space, a mask of pixels that likely contain a volume fraction of GM is subtracted from the aCompCor masks. This mask is obtained by dilating a GM mask extracted from the FreeSurfer's aseg segmentation, and it ensures components are not extracted from voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original

implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al. 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance timeseries are calculated by means of principal components analysis of the signal found within a thin band (crown) of voxels around the edge of the brain, as proposed by Patriat, Reynolds, and Birn 2017). All resamplings can be performed with a single interpolation step by composing all the pertinent transformations (i.e., head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using nitransforms, configured with cubic B-spline interpolation. All functional volumes were smoothed with a Gaussian kernel with an FWHM of 8 × 8 × 8 mm.

## 11.FRENCH AND PORTUGUESE SECTION

#### 11.1. Resumo

Interagimos diariamente com objetos em nosso ambiente imediato, fisicamente próximos e sobre os quais uma ação pode ser exercida. Esses objetos situam-se em nosso espaço peripessoal (PPS), um espaço que funciona como uma interface motora entre o corpo e o ambiente, facilitando assim a interação. Os objetos presentes no PPS são automaticamente codificados em termos sensório-motores, como se o organismo antecipasse uma interação com eles. No entanto, os objetos localizados em nosso PPS nem sempre nos pertencem, e nem sempre é possível interagir com eles. Essa situação pode gerar um conflito entre (1) a codificação sensório-motora dos objetos, que contribui para a preparação da ação em direção aos objetos alcançáveis no PPS, e (2) a codificação conceitual baseada na propriedade, que indica que certas interações são favorecidas, enquanto outras são proibidas. Nesse contexto, a interação entre o PPS e a propriedade no processamento de objetos ainda é pouco compreendida.

Para examinar essa hipótese, uma série de estudos comportamentais e de neuroimagem foi conduzida utilizando tarefas de julgamento de alcançabilidade. Os participantes deviam avaliar se objetos pertencentes a si mesmos ou a outra pessoa eram alcançáveis quando colocados a diferentes distâncias. O primeiro estudo forneceu evidências comportamentais de uma interação entre propriedade e espaço: tempos de resposta mais rápidos foram observados para os objetos pertencentes ao próprio participante. Esse efeito de facilitação era limitado ao PPS e foi acompanhado por uma expansão do limite percebido do espaço alcançável. O segundo estudo precisou essa interação, mostrando que um melhor controle inibitório, favorecendo uma ação mais eficiente, era facilitado para objetos possuídos localizados no PPS. Por fim, o terceiro e o quarto estudos evidenciaram os correlatos temporais e neurais dos efeitos observados. Os dados de EEG

mostraram que o PPS influenciava os processamentos perceptivos precoces, enquanto a propriedade afetava etapas mais tardias, pós-perceptivas, sugerindo um processo sequencial que vai do codificação espacial à integração de informações conceituais de ordem superior. Os resultados de fMRI revelaram que os objetos situados no PPS ativavam regiões parietais envolvidas no processamento sensório-motor, com respostas mais fortes para os objetos pertencentes a si do que para os pertencentes a outros. Além disso, mostraram que as ativações do córtex pré-frontal medial ventral e dorsal (mPFC) codificam de forma diferenciada os objetos possuídos, dependendo do contexto experimental.

Em conjunto, esses resultados demonstram que o processamento de objetos no PPS não é regido apenas por sua proximidade física ou saliência perceptiva, mas também é modulado por fatores de ordem superior, como a propriedade. Nesse sentido, dentro do PPS, a propriedade constitui uma pista contextual que modula a seleção da ação, orientando não apenas para o que é físicamente acessível, mas também para o que é socialmente relevante.

<u>Palavras-chave</u>: espaço peripessoal, sentido de propriedade dos objetos, acoplamento percepçãoação, contexto social, EEG, EMG, fMRI.

#### 11.2. RÉSUMÉ

Nous interagissons quotidiennement avec des objets dans notre environnement immédiat, physiquement proches et sur lesquels une action peut être exercée. Ces objets se situent dans notre espace péripersonnel (PPS), un espace qui sert d'interface motrice entre le corps et l'environnement, facilitant ainsi l'interaction. Les objets présents dans le PPS sont automatiquement encodés en termes sensorimoteurs, comme si l'organisme anticipait une interaction avec eux. Toutefois, les objets situés dans notre PPS ne nous appartiennent pas toujours, et il n'est pas toujours possible d'interagir avec eux. Cette situation peut engendrer un conflit entre (1) le codage sensorimoteur des objets, qui contribue à la préparation de l'action vers des objets atteignables dans le PPS, et (2) le codage conceptuel fondé sur la propriété, qui indique que certaines interactions sont favorisées, tandis que d'autres sont interdites. Dans ce contexte, l'interaction entre le PPS et la propriété dans le traitement des objets demeure encore mal comprise.

Afin d'examiner cette hypothèse, une série d'études comportementales et de neuroimagerie a été menée en utilisant des tâches de jugement d'atteignabilité. Les participants devaient évaluer si des objets, appartenant à soi ou à autrui, étaient atteignables lorsqu'ils étaient placés à différentes distances. La première étude a fourni des preuves comportementales d'une interaction entre la propriété et l'espace : des temps de réponse plus rapides ont été observés pour les objets appartenant à soi. Cet effet de facilitation était limité au PPS et s'accompagnait d'une expansion de la limite perçue de l'espace atteignable. La deuxième étude a précisé cette interaction en montrant qu'un meilleur contrôle inhibiteur, favorisant une action efficace, était facilité pour les objets possédés situés dans le PPS. Enfin, les troisième et quatrième études ont mis en évidence les corrélats temporels et neuronaux des effets observés. Les données EEG ont montré que le PPS influençait les traitements perceptifs précoces, tandis que la propriété affectait des étapes plus

tardives, post-perceptives, suggérant un processus séquentiel allant de l'encodage spatial à l'intégration d'informations conceptuelles de plus haut niveau. Les résultats d'IRMf ont révélé que les objets situés dans le PPS activaient les régions pariétales impliquées dans le traitement sensorimoteur, avec des réponses plus fortes pour les objets appartenant à soi que pour ceux appartenant à autrui. De plus, ils ont montré que les activations du cortex préfrontal médian ventral et dorsal (mPFC) codent différemment les objets possédés, selon le contexte expérimental.

Dans leur ensemble, ces résultats démontrent que le traitement des objets dans le PPS n'est pas uniquement régi par leur proximité physique ou leur saillance perceptive, mais qu'il est également modulé par des facteurs de plus haut niveau, tels que la propriété. Dans ce cadre, au sein du PPS, la propriété constitue un indice contextuel qui module la sélection de l'action, en orientant non seulement vers ce qui est physiquement accessible, mais aussi vers ce qui est socialement pertinent.

<u>Mots-clés</u>: espace péripersonnel, sens de la propriété des objets, couplage perception-action, contexte social, EEG, EMG, IRMf.

### 11.3. Introduction

La présente section vise à introduire la partie francophone de cette thèse, qui regroupe un ensemble de travaux consacrés à la compréhension des mécanismes neurocognitifs par lesquels l'espace péripersonnel (PPS) et le sens de la propriété des objets interagissent pour structurer la cognition incarnée. Le PPS, défini comme l'espace immédiatement entourant le corps dans lequel une interaction physique directe avec les objets est possible, constitue un champ d'investigation privilégié pour comprendre la manière dont le cerveau intègre les informations relatives au corps et à l'environnement dans une perspective orientée vers l'action. Traditionnellement conçu comme une interface sensorimotrice flexible, le PPS soutient à la fois des fonctions défensives et d'approche, en s'adaptant de manière dynamique au contexte physique et social.

Dans ce cadre, l'objectif principal de cette thèse a été d'examiner dans quelle mesure des dimensions sociales abstraites comme le sens de la propriété des objets (aussi appelé *ownership* des objets) influencent les mécanismes de traitement sensorimoteur au sein du PPS. En effet, l'ownership ne se réduit pas à une simple relation juridique ou sémantique : elle constitue un marqueur de signification à la fois personnelle et sociale, capable de conférer aux objets une valeur autoréférentielle. L'incorporation cognitive d'objets possédés (*self-owned*), décrite dès William James (1890) et reprise par Belk (1988), suggère que les objets appartenant au soi sont traités comme une extension de ce dernier. Or, lorsque ces objets sont situés à proximité du corps, la convergence entre les dimensions spatiales et sociales (qu'elles aillent dans le même sens ou qu'elles soient conflictuelles) pourrait engendrer des biais spécifiques impactant les mécanismes sensorimoteurs impliqués dans le traitement des objets pour les actions dirigées vers un but.

Pour tester cette hypothèse, quatre études expérimentales, combinant approches comportementales, électrophysiologiques (EMG et EEG) et d'imagerie fonctionnelle (IRMf), ont

été menées. Celles-ci visaient à déterminer comment la propriété des objets module : (1) la frontière fonctionnelle du PPS, (2) les dynamiques temporelles de traitement des objets selon leur appartenance, et (3) les mécanismes neuraux sous-tendant l'intégration conjointe des informations spatiales et sociales. L'ensemble de ces travaux repose sur des tâches de jugement d'atteignabilité (un paradigme habituellement utilisé pour étudier la représentation du PPS et les mécanismes associés en contexte d'interaction avec les objets), permettant d'accéder à la dimension motrice implicite du traitement des objets. À travers cette approche, la thèse ambitionne de proposer un modèle unifié du PPS comme espace d'action socialement structuré, où les représentations du corps et de l'environnement s'articulent en fonction de la pertinence sociale et normative des objets.

### 11.4. ETUDE 1

## 11.4.1. Avant-propos

Le PPS fonctionne comme une interface spécialisée à la fois pour les interactions dirigées vers les objets et pour les interactions sociales, et ses dimensions se trouvent modulées par divers facteurs. Cependant, malgré des avancées majeures dans la compréhension des influences exercées par les variables liées aux objets et aux interactions sociales sur la plasticité du PPS, aucune étude n'a encore examiné la manière dont ces deux types d'informations peuvent interagir. Cette question revêt une importance particulière dans la mesure où l'information sociale peut être incarnée non seulement par d'autres individus, mais également par les objets eux-mêmes, qui incarnent souvent des informations relatives à leur propriété dans la vie quotidienne.

Nous avons formulé l'hypothèse selon laquelle être propriétaire d'un objet facilite le traitement des objets situés dans le PPS, c'est-à-dire dans la zone où les actions sont directement

possibles. Plus précisément, à l'aide d'une tâche de jugement d'atteignabilité, nous nous attendions à observer des temps de réaction plus rapides pour les objets appartenant à soi que pour ceux appartenant à autrui, mais avec un effet de facilitation limité aux objets placés dans le PPS. De plus, nous avons prédit que, pour les distances où la tâche de jugement d'atteignabilité est plus difficile (notamment à la frontière du PPS), être le propriétaire de l'objet agirait comme un indice supplémentaire facilitant la prise de décision motrice, entraînant ainsi un biais décisionnel qui étendrait la frontière perçue du PPS.

Par ailleurs, en considérant que la propriété pourrait être encodée ou influencer le traitement des objets de manière différente selon les capacités sociales individuelles, nous avons examiné si les différences d'empathie corrélaient avec la modulation, induite par la propriété, de la frontière du PPS. Enfin, de manière exploratoire, nous avons également étudié si l'interaction entre la localisation spatiale et la propriété influençait le cadre de référence spatial (e.g., égocentrique ou allocentrique) utilisé pour encoder les informations relatives aux objets.

## 11.4.2. Résumé

Dans le chapitre 4, la première expérience a examiné comment la propriété influence la représentation et le traitement des objets dans l'espace péripersonnel (PPS) d'un point de vue comportemental. Les participants sélectionnaient une tasse comme leur appartenant, tandis qu'une autre tasse était attribuée à un personnage virtuel visible dans l'environnement. Ils devaient ensuite estimer si ces deux tasses étaient atteignables lorsqu'elles étaient placées à différentes distances sur une table virtuelle.

Les temps de réponse lors de la tâche de jugement d'atteignabilité étaient significativement plus rapides pour les tasses appartenant à soi que pour celles appartenant à autrui, mais uniquement

lorsqu'elles se situaient dans le PPS. Dans l'espace extrapersonnel (EPS), cet avantage disparaissait. De plus, les jugements d'atteignabilité étaient biaisés : les participants estimaient pouvoir atteindre leur propre tasse à une distance plus grande que celle de l'autre, entraînant une extension de la frontière du PPS pour les objets appartenant à soi. Fait intéressant, cette expansion corrélait avec les scores à la sous-échelle « Fantasy » de l'IRI (Davis, 1983), suggérant que les individus ayant une plus grande facilité à s'engager dans des situations imaginaires ou virtuelles étaient plus sensibles aux biais induits par notre manipulation expérimentale.

Après chaque jugement, les participants localisaient la position de la tasse, tandis que le personnage virtuel était déplacé subrepticement. Des erreurs de localisation survenaient principalement pour les objets situés dans l'EPS, indépendamment de la propriété, ce qui implique qu'une focalisation attentionnelle à distance induisait un passage d'un cadre de référence égocentrique à un cadre allocentrique. En résumé, ce chapitre fournit des preuves comportementales démontrant que les objets appartenant à soi dans le PPS bénéficient d'un traitement prioritaire : les actions dirigées vers les tasses possédées sont planifiées plus rapidement, et la frontière péripersonnelle s'étend lorsque ces objets constituent les stimuli disponibles.

## 11.5. ETUDE 2

## 11.5.1. Avant-propos

Dans l'étude précédente, nous avons observé que les jugements d'atteignabilité étaient facilités pour les objets appartenant à soi comparativement à ceux appartenant à autrui, mais uniquement dans le PPS, c'est-à-dire dans la zone où les actions sont directement exécutables. À la suite de cette observation, nous avons formulé l'hypothèse que cette facilitation (assimilable à une forme de priorisation contextuelle des informations relatives à soi), limitée à l'espace d'action,

servirait à accroître l'efficacité des actions dirigées vers les objets dont nous sommes propriétaires, et se manifesterait vraisemblablement au cours de processus spécifiquement moteurs.

Afin de tester cette hypothèse, l'étude suivante a exploré l'interaction entre la propriété et la localisation spatiale dans les processus d'inhibition motrice en ligne, fortement impliqués dans le fait de sous-tendre des actions efficaces. Nous avons proposé que si la priorisation contextuelle des informations relatives à soi mentionnée précédemment favorise l'efficacité de l'action lorsque pertinent, elle devrait se manifester non seulement par des réponses plus rapides, mais aussi par une suppression plus efficace et plus rapide des activations motrices erronées lors des interactions avec des objets dont nous sommes propriétaires, comparativement aux objets dont autrui est propriétaire. À cette fin, nous avons enregistré l'activité électromyographique (EMG) des muscles de la main impliqués dans la réponse. Cette méthode nous a également permis d'observer les différentes phases du mouvement engagées dans la réponse, et ainsi d'examiner si la facilitation précédemment observée dans les temps de réaction apparaissait au moment de l'exécution motrice (« temps moteur ») ou précédait cette exécution (« temps prémoteur »).

Il est important de souligner que notre objectif principal était de créer un conflit entre deux types d'informations (spatiales et liées à l'ownership) afin de provoquer des erreurs motrices, d'une manière analogue à celle des tâches d'interférence telles que la tâche de Stroop. Pour ce faire, nous avons d'abord mené une expérience en ligne comprenant (i) une tâche de jugement de propriété et (ii) une tâche de jugement d'atteignabilité, afin de déterminer quel facteur était traité en premier et, par conséquent, le plus susceptible d'influencer l'autre. Cette étude préliminaire nous a également permis d'observer si le schéma des temps de réaction observé dans le chapitre 4 se reproduisait en ligne, dans différentes conditions expérimentales.

### 11.5.2. Résumé

Cette seconde expérience a utilisé l'EMG de surface pour examiner l'influence de la propriété sur le contrôle moteur à travers l'inhibition exécutive. Nous avons enregistré l'activité musculaire du pouce lors d'une tâche adaptée de jugement d'atteignabilité afin de détecter les activations motrices précoces et de suivre la correction des erreurs.

Les enregistrements EMG ont également permis d'étudier la proportion d'erreurs partielles (c'est-à-dire de petites activations erronées corrigées en ligne) comme indice d'efficacité du contrôle inhibiteur. Pour les objets situés dans le PPS, les réponses correctes à destination des tasses appartenant à soi étaient initiées, sur la base de l'activité musculaire, plus rapidement que celles dirigées vers les tasses appartenant à autrui, confirmant les résultats de la première expérience. À l'inverse, dans l'EPS, la tendance s'inversait (les objets appartenant à autrui entraînaient des latences légèrement plus courtes que ceux appartenant à soi, bien que les réponses globales y soient plus lentes). Ce schéma se retrouvait également dans les temps de réaction comportementaux, indiquant que la localisation spatiale et la propriété interagissent pour modeler à la fois les initiations et les réponses motrices.

Une analyse temporelle des erreurs initiées (réponses erronées en fonction de la position spatiale du stimulus) a révélé que la différence de fréquence d'erreurs entre les objets appartenant à soi et à autrui, dans le PPS comme dans l'EPS, ne pouvait pas être attribuée à des réponses rapides et impulsives. Au contraire, cette divergence augmentait au fil du temps, suggérant une influence progressive et cumulative de la propriété : à mesure que la fenêtre de réponse s'allongeait, les participants semblaient de plus en plus biaisés par une inhibition liée au sens de la propriété, suggérant un phénomène robuste et difficile à ignorer. De plus, la majorité des erreurs initiées étaient corrigées en ligne, et la correction motrice était significativement plus efficace et

rapide pour les objets appartenant à soi que pour ceux appartenant à autrui dans le PPS, tandis que cet effet n'était pas observé dans l'EPS. Cela suggère un recrutement plus fort des processus rapides d'inhibition et d'ajustement pour les stimuli pertinents pour le soi dans le PPS. Dans l'ensemble, la présence d'un « schéma en miroir » dans plusieurs mesures (c'est-à-dire des réponses plus rapides pour les objets appartenant à autrui dans l'EPS) suggère un compromis spatial : chaque cible s'aligne préférentiellement sur l'espace d'action pertinent de l'agent concerné (soi dans le PPS, autrui dans l'EPS). Cependant, le fait que les objets appartenant à soi dans le PPS entraînent des corrections plus efficaces indique un avantage du soi robuste dans le PPS aux premiers stades du contrôle moteur.

### 11.6. ETUDE 3

## 11.6.1. Avant-propos

Dans les chapitres 4 et 5, nous avons caractérisé l'interaction entre le sens de la propriété des objets et leur localisation spatiale. Nous avons montré que la priorisation des objets appartenant à soi était contextuelle et dépendait de la position de l'objet au sein du PPS accessible à l'action. Nous avons également observé que le contrôle inhibiteur était renforcé pour les objets appartenant à soi situés dans le PPS, suggérant qu'être le propriétaire d'un objet optimise les mécanismes de sélection et de correction de l'action dans cet espace. Fait intéressant, dans certains cas, un schéma de priorisation inverse est apparu, avec des temps de réaction plus courts pour les objets appartenant à autrui dans l'EPS. Ces résultats mettent clairement en évidence une interaction entre la localisation spatiale et la propriété ; toutefois, la manière et le moment précis où ces deux facteurs interagissent dans le traitement des objets demeurent incertains. Cette interaction se manifeste-t-elle à un instant unique, reflétant l'émergence d'un mécanisme unifié, ou traduit-elle

l'influence séquentielle de mécanismes distincts intervenant à différentes étapes du traitement cognitif ?

Pour répondre à cette question, l'étude suivante a utilisé l'électroencéphalographie (EEG) afin d'examiner la dynamique temporelle de cette interaction au cours d'une tâche de jugement d'atteignabilité. Étant donné que l'encodage du PPS et la priorisation du soi ont tous deux été associés à des mécanismes perceptifs précoces (comme en témoignent des composantes ERP telles que la N1) ainsi qu'à des processus décisionnels plus tardifs (reflétés par la composante P3), nous avons examiné un ensemble de potentiels évoqués susceptibles d'être modulés à la fois par l'espace et par la propriété, afin d'identifier quand et comment ces deux facteurs influencent le traitement des stimuli.

## 11.6.2. Résumé

Dans ce chapitre, nous avons utilisé l'EEG afin d'examiner la dynamique temporelle du traitement des objets dans le PPS et l'EPS en fonction du sens de la propriété des objets. Les participants réalisaient de nouveau la tâche de jugement d'atteignabilité avec des objets appartenant à soi ou à autrui, face à un personnage virtuel.

Les potentiels évoqués (ERP) ont révélé une stratification temporelle claire : les composantes perceptives précoces (N1) et sensori-motrices (N2 antérieure) étaient sensibles à la localisation spatiale de l'objet, mais non à la propriété, présentant respectivement des composantes plus précoces et plus amples pour les objets situés dans le PPS que dans l'EPS. En revanche, les composantes ERP de latence moyenne à tardive reflétaient le contenu social à travers la propriété : la composante P3 était amplifiée pour les objets appartenant à soi (mais uniquement dans le PPS), et une négativité antérieure de type N400, typiquement associée à une violation sémantique ou

sociale, était plus marquée pour les objets appartenant à autrui dans le PPS. Ces résultats indiquent que la proximité spatiale intervient au niveau du traitement perceptif précoce, où les objets proches sont automatiquement traités plus rapidement, tandis que l'information liée à la propriété exerce son influence à des stades post-perceptifs plus tardifs.

## 11.7. ETUDE 4

# 11.7.1. Avant-propos

Les résultats présentés jusqu'à présent ont démontré que la propriété des objets et leur localisation spatiale interagissent lors du traitement des objets en vue d'une action efficace, notamment à travers des mécanismes d'origine motrice. Dans le chapitre 6, nous avons observé que cette interaction suivait une séquence temporelle : l'information spatiale, en particulier la présence d'un objet dans le PPS, influençait le traitement à un stade perceptif précoce, tandis que l'information relative à la propriété était intégrée ultérieurement. La propriété de soi était effectivement priorisée à un stade post-perceptif voire décisionnel, alors que la propriété d'autrui était intégrée au cours d'une évaluation contextuelle.

Cependant, les corrélats neuronaux de cette interaction demeurent à préciser. Les travaux antérieurs ont associé le traitement de l'information dans le PPS à l'activité d'un réseau frontopariétal incluant le cortex prémoteur et les régions pariétales postérieures, en particulier le sillon intrapariétal. En revanche, le traitement de la propriété des objets et de la pertinence de soi a été associé à des activations dans les régions médiales du cortex préfrontal (mPFC), avec des distinctions fonctionnelles entre ses subdivisions dorsale et ventrale, cette dernière étant souvent considérée comme une aire centrale pour le traitement autoréférentiel.

L'étude en IRMf présentée ci-après visait à déterminer comment ces réseaux distincts, mais potentiellement interconnectés, contribuent au traitement des objets appartenant à soi ou à autrui

lorsqu'ils sont situés dans l'espace proche ou lointain. Nous avons formulé l'hypothèse que si la priorisation des objets appartenant à soi dans le PPS reflète l'intégration d'informations spatiales et socio-conceptuelles en vue de préparer une action possible, alors une modulation du réseau fronto-pariétal associé au PPS devrait être observée. Un second objectif consistait à déterminer si l'implication du cortex préfrontal médian ventral (mPFC ventral) dans le traitement des informations liées au soi (et, dans une moindre mesure, du mPFC dorsal dans le traitement des informations liées à autrui) est obligatoire et constante à travers les contextes, ou si elle est modulée par la pertinence contextuelle.

### 11.7.2. Résumé

Finalement, dans la dernière étude présentée dans ce chapitre, nous avons examiné les activations neuronales associées à l'interaction entre l'espace et la propriété. Les participants ont passé une session d'IRMf tout en effectuant une version adaptée de la tâche de jugement d'atteignabilité.

Lorsque les participants jugeaient des objets atteignables dans le PPS, des activations bilatérales étaient observées dans le cortex pariétal, en particulier autour de la portion antérieure du sillon intrapariétal (aIPS). Dans le PPS, ces régions étaient particulièrement sollicitées lors des jugements d'atteignabilité des objets appartenant à soi, comparativement à ceux appartenant à autrui. En revanche, les objets situés dans l'EPS suscitaient une activation plus marquée dans les régions médiales du cortex préfrontal, connues pour leur implication dans la cognition sociale, possiblement en lien avec la présence du personnage virtuel. De plus, une analyse de formes multivoxel (multi-voxel pattern analysis, MVPA) a révélé que l'activité dans la portion ventrale du cortex préfrontal médian (mPFC ventral) encodait spécifiquement les objets appartenant à soi dans

le PPS, tandis que l'activité dans la portion dorsale du mPFC suivait spécifiquement les objets appartenant à soi à la fois dans le PPS et dans l'EPS. Ces résultats suggèrent que l'estimation de l'atteignabilité des objets dépend de régions spécialisées dans l'encodage des capacités d'action du corps dans l'espace ainsi que des informations pertinentes pour le soi et socialement signifiantes : les régions pariétales signaleraient les actions possibles, tandis que le mPFC indiquerait quels objets sont pertinents pour le soi et, par conséquent, disponibles pour l'action.

#### 11.8. Conclusion

Les travaux présentés dans cette thèse invitent à repenser la conception classique de l'espace péripersonnel. Loin de se limiter à une interface définie par la proximité physique ou la simple possibilité physique d'une action, le PPS apparaît comme un espace où les contraintes sociales, normatives et contextuelles influencent directement la représentation et la sélection des actions. La propriété d'un objet, à la fois en tant qu'indice social de contrôle et que marqueur du self, agit ici comme un facteur contextuel déterminant, modulant la dynamique sensorimotrice selon que l'objet est perçu comme appartenant au soi ou à autrui.

Cette perspective élargie conduit à envisager le PPS comme un espace d'action socialement structuré, où les possibilités d'action sont pondérées non seulement par des contraintes physiques, mais également par des considérations sociales et normatives. Ainsi, l'intégration de la propriété dans le traitement spatial révèle que les processus sensorimoteurs impliqués dans le traitement des objets dans le PPS sont biaisés par les interactions entre le soi, l'environnement et autrui qui reposent sur une hiérarchisation dynamique dépendante à la fois de la distance corporelle et de la signification sociale des objets.

Sur le plan théorique, cette thèse propose donc d'abandonner une vision strictement proxémique (ou relative à la prédiction du contact) du PPS au profit d'un modèle sensible au contexte, où les représentations spatiales intègrent des informations conceptuelles et sociales. Sur le plan prospectif, ces travaux ouvrent la voie à de nouvelles recherches explorant la manière dont les interactions sociales, la présence d'autrui ou la co-action façonnent la représentation de l'espace d'action. En définitive, l'étude conjointe du PPS et de l'ownership contribue à une compréhension plus complète de la manière dont le cerveau humain intègre les dimensions physiques et sociales pour guider le comportement dans des environnements complexes et socialement signifiants.