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The Unconscious Self

How the brain encodes bodily-self visual cues in the absence of awareness

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Abstract

We constantly experience ourselves as inherently tied to our conscious experience and to our own body. The nature of self-consciousness has long captivated thinkers across disciplines, sparking debates on its functions and meaning in philosophy, and its underlying brain mechanisms in neuroscience. On one side, consciousness seems to be mainly characterized by its holistic and integrated nature. On the other side, unconscious processing operates at lower cognitive levels, handling predictable and automatic processes crucial for survival. Whitin this framework, bodily-self processing should be intrinsically important for survival, considering that it represents the physical substrate of one's existence and a spatial reference for environmental interactions. However, less is known about how our bodily self is processed in relation to consciousness. Is it possible that some aspects of bodily self-processing might precede conscious perception?

This dissertation investigates the relationship between bodily self and visual awareness, exploring how identity-related visual stimuli are encoded without awareness and prioritized by the brain into conscious perception. Two primary research lines were pursued: one focusing on hand bodily stimuli, whether the second focused on face identity processing. Specifically, the first research line examined how spatial perspective and visual identity of hand stimuli affect visual awareness, and whereas it is possible to trigger unconscious body ownership when bodily self-consciousness constraints are respected. The second research line explored face identity processing and its relation to visual awareness by investigating the relation between self-face perception and electrophysiological correlates of visual awareness, and by investigating unconscious face identity processing in a patient affected by hemianopia and prosopagnosia following brain damages.

Across five studies, this work provides evidence that certain aspects of the bodily self might not necessitate conscious processing and can directly influence visual awareness. Together, these

findings support a hierarchical self-model, where lower-order self-representations operate unconsciously, forming the foundation for higher-order, integrated self-consciousness. This work emphasizes the unconscious, predictable, and relevant nature of bodily self-processing, while highlighting the role of consciousness in resolving ambiguities that might challenge bodily self-consciousness constructs.

Table of Contents

Chapter I 1

On the Conscious, the Unconscious and the Self 1

1.1 *Introduction* **1**

1.2 *Aim and structure of the thesis* **7**

1.3 *Main Methodologies for the study of visual awareness* **8**

Chapter II 14

On the relation between the Bodily-Self and Visual Awareness 14

2.1 *General Introduction* **14**

2.2 ***Study 1*****: Spatial Perspective and Identity in Visual Awareness of the bodily self-other distinction** 17

2.2.1 *Introduction* **17**

2.2.2 *Methods* **19**

2.2.3 *Results* **22**

2.2.4 *Discussion* **23**

2.2.5 *Interim Conclusions* **26**

2.3 ***Study 2*****: The role of identity Priming on the (unconscious) bodily-self Attribution** 28

2.3.1 *Introduction* **28**

2.3.2 *Methods* **29**

2.3.3 *Results* **32**

2.3.4 *Discussion* **33**

2.3.5 *Interim Conclusions* **37**

2.4 ***Study 3*****: Visual Awareness is not required for the Virtual Hand Illusion: a combined protocol of Virtual Reality and Continuous Flash Suppression** 38

2.4.1 *Introduction* **38**

2.4.2 *Methods* **41**

2.4.3 *Results* **50**

2.4.4 *Discussion* **52**

Chapter III 56

On Face Identity processing in the absence of Awareness 56

3.1 *Face familiarity* **56**

3.2 *Face Familiarity and Awareness* **59**

3.3 ***Study 4*****: Visual Awareness Negativity is modulated by facial identity** 64

3.3.1 *Introduction* **64**

3.3.2 *Methods* **67**

3.3.3 *Results* **71**

3.3.4 *Discussion* **74**

3.4 ***Study 5*****: Unconscious face familiarity processing in a patient with Hemianopia and Acquired Prosopagnosia: A Single Case Study** 78

3.4.1 *Introduction* **78**

3.4.2 *Methods* **82**

3.4.3 *Results* **91**

3.4.4 *Discussion* **94**

Chapter IV 99

4.1 *Summary of main findings of Hands Awareness studies* **99**

4.2 *Summary of main findings of Face Awareness studies* **102**

4.3 ***General Conclusion*** **104**

References 108

Chapter I

On the Conscious, the Unconscious and the Self

'Having a self, even a simple self, allows you to look into the world and put a mark over what is more important and less important. It's a way of classifying the world in terms of your own needs.'

Antonio Damasio

1.1 *Introduction*

The concept of *Self-Consciousness* is something for which philosophers, psychologists, scientists, and almost everyone, me included, struggled for centuries. A wide range of definitions, divisions, reflections, functions, have been generated by such a jubilation of thoughts. Renè Descartes defined consciousness (from Latin, '*com*' + '*shire*', '*with' + 'knowledge*') as '*a subjective experience, foundation of our (explicit) knowledge and self-awareness, inseparable from thinking, and evidence of existance*', whereas Thomas Nagel defined it as '*the ability to experience and to feel the subjective existance*'. Both the definitions mostly focus on the fact that consciousness is extremely tied on the subjective experiencing of the inner mind. With advancements in technology enabling the observation of brain activity across different states of consciousness or content of consciousness (Dehaene & Changeux, 2011), these questions are gradually shifting from the philosophical to neuroscientific domain, as we are almost certain that the subjective experience of consciousness arises through brain activity. Epistemologically, some issues remain scientifically difficult to investigate (the so-called 'hard problems', as explaining *how* and *why* the subjective phenomenal feeling of experience - *qualia* (Dennett, 1993) - arises), while others are more accessible ('easy problems', as explaining the mechanisms supporting consciousness; Block, 1995; Chalmers, 1996; Chalmers, 1995) to the scientific method. Although highly speculative and with the lack of clearly shared definitions in the scientific community, nowadays neuroscience seems less prone to the study of *Self-Consciousness*

intended as the subjective feeling to be a unique organism within a coherent continuum of experiences tied to the self, being at the same time the object and the subject of such experience - rather, it seems more focused in the study of consciousness per sè (i.e., what makes us 'aware' in our state of consciousness, or what allows us to have a conscious experience). The biggest challenge of the last two decades (and likely also of the next years) relies on the search for the *locus* of Consciousness and its neural substrate, i.e., the neural correlates of Consciousness (NCC), that have been defined as 'the minimal set of neuronal events and mechanisms jointly sufficient for a specific conscious percept' (Koch, 2004). Many theories have been proposed, each with considerable orthogonal disagreement regarding the underlying brain network responsible for consciousness (Dembski et al., 2021; Seth & Bayne, 2022; **Fig. 1.1**). For instance, two of the main leading theories, the Global Workspace Theory (GWT; Mashour et al., 2020) and the Integrated Information Theory (IIT; Boly et al., 2017; Tononi et al., 2016), posit fundamentally opposing NCCs, such as the prefrontal-parietal network compared to posterior areas, respectively. Curiously, if one would merge all the NCCs from all the different Theories of Consciousness, almost all the brain would result to be involved (Yaron et al., 2022).

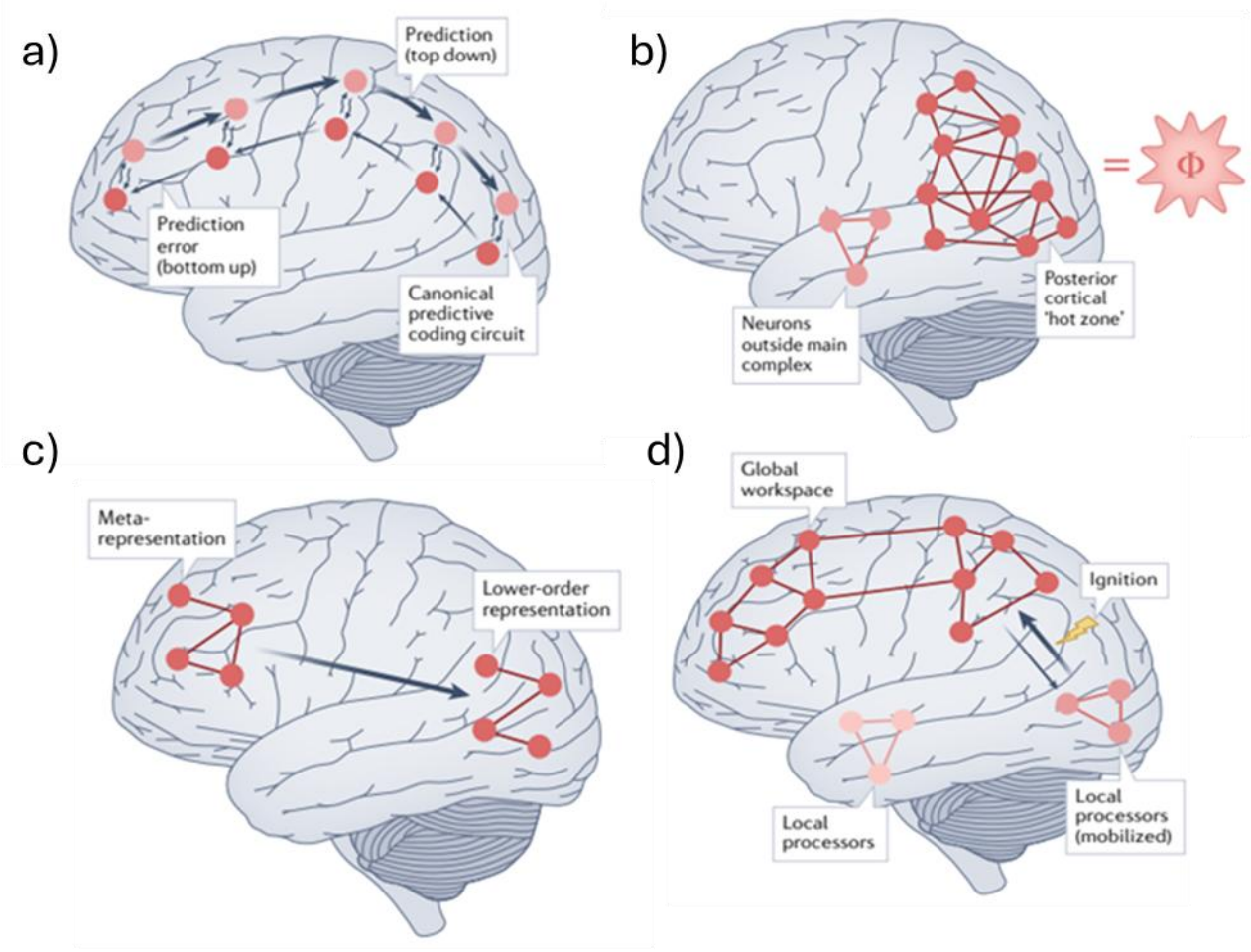

Figure 1.1*: This image was taken and adapted from Seth and Bayne, 2022. It represents brain mechanisms jointly sufficient and necessary for consciousness accordingly to the most influential theories of consciousness. a) Predictive Processing and Recurrent processing Theories, assuming that consciousness arises from top-down predictive or recurrent processing. b) Integrated Information Theory, assuming that consciousness arises through posterior brain activity and it is directly related to complexity of information integration, that can be measured and expressed as phi (Φ). c) High-Order Theories, expressing consciousness as meta-representational states having other representations as targets. d) Global Workspace Theories, assuming that consciousness arises when information is broadcasted within the global workspace (the fronto-parietal network) by local processors through the ignition process, that amplifies and sustains representations.*

Current Theories of Consciousness might not agree at all on its NCC, but they mainly agree on the fact that consciousness is particularly related to the integration of brain information to certain

extents (i.e., the GWT, the IIT, high-order theories; Deroy et al., 2016; Faivre et al., 2015a; Lau & Rosenthal, 2011; Zher-Wen & Yu, 2023a), that integration is needed for consciousness and vice versa (Mudrik et al., 2014), as the conscious experience is not fragmented but rather intrinsically holistic and unified. Whereas consciousness is certainly not a *conditio sine qua non* for complexity, complexity might be a *conditio sine qua non* for consciousness: many theories argues that it requires a certain level of brain complexity to emerge (Casarotto et al., 2016; Tononi et al., 2016). For instance, theories like the GWT and IIT support the fact that consciousness arises when information processing is integrated across a complex brain network. By contrast, complex systems, like artificial networks, can exhibit highly intricate behaviors without being conscious (Bayne et al., 2024). But how can we find the network subserving consciousness? To identify the neural substrates that are 'strictly necessary and sufficient' for consciousness, it is essential to map and differentiate brain areas and cognitive functions that operate without awareness - that is, unconsciously. Indeed, a complementary and necessary approach to the study of consciousness relies on the investigation of correlates and functional properties of unconscious processes, exploring its capacities, limitations, and scopes, as conscious processing must be contrasted with comparable unconscious processing (Doerig et al., 2021; Hesselmann, 2019; Kouider & Dehaene, 2007; Stein, 2019; Stein & Peelen, 2021). In the context of cognitive neuroscience, unconscious processing has been defined as the '*referring to the automatic and involuntary handling of information by the brain, occurring without conscious awareness, yet capable of influencing perception, cognition, and behavior'* (Kouider & Dehaene, 2007). In experimental neuroscience, trials are classified as conscious or unconscious concerning experiment manipulations, and differences in brain activity are considered the neural correlates of consciousness. The logical rationale is that if I perform a certain cognitive function or if a neural population spikes independently of awareness, then it must not be necessary for consciousness and its neural correlates. However, even the functional properties and scope of unconscious processing have been marked by contrasting theories at the philosophical, neuroscientific and methodological levels (Chalmers, 1996; Hesselmann & Moors, 2015; Marcel, 1983; Newell & Shanks, 2014;

Schmidt, 2015; Stein & Peelen, 2021). For example, the mentalistic account posed in favor of a 'dumb' unconscious processing, affirming that non-conscious processes are non-representational and cannot involve high-level processing (i.e., Loftus & Klinger, 1992); other accounts proposed the vision of a smart unconscious, as '*non-conscious perceptual processes automatically redescribe sensory data into every representational form and to the highest levels of description available to the organism'* (Marcel, 1983, p.238). On one side, unconscious processing is mostly considered a dumb, low-level driven system; on the other it is seen as a smart system capable of high-level cognitive processing (Hassin, 2013; Hesselmann, 2019; Hesselmann & Moors, 2015; Moors et al., 2017). Such disagreements are likely to arise from differences in the methodological approach for studying unconscious processing and differences in defining the phenomenon under investigation. To date, the scenario emerging from a plethora of paradigms and studies seems to suggest that unconscious cognition is closely linked to low-level types of processing (i.e., sensory encoding) and mostly 'isolated' with respect to information integration, in contrast to conscious cognition which operates at higher cognitive levels. However, even if consciousness has a pivotal role in the integrative process of brain information, some forms of integration might nevertheless be independent from conscious processing. Although speculative and simplistic, there is consensus about the fact that consciousness is mostly related to responding to highly complex and unpredictable situations, to flexibly adjust behavior facing novel contexts (Baars et al., 2013; Cheesman & Merikle, 1986; Dehaene, 2001a; Searle, 1992) for metacognition, cognitive planning, and for understanding other's mind and intentions (Cleeremans, 2005; Crick & Koch, 2003; Koch & Tsuchiya, 2007; Velmans, 2003), i.e., very essential cognitive processes for human's life. What would be then the role of unconscious processing, if not to cover all the other processing that might not require the involvement of expensively higher conscious resources? As a matter of fact, most of the brain processes take place without our awareness. We can breathe, we can move, and sometimes we can even drive without us being conscious of it – in a way, if humans automatize certain behaviors, then the limited and expensive conscious resources might not be necessary anymore for their implementations. Indeed, in

contrast to the 'main' role of consciousness, all the situations that would be highly predictable, highly automatic, but also such processing that could be of extreme relevance for survival, might take place without the involvement of consciousness. As consciousness resources are limited (Dehaene & Changeux, 2011; Marois & Ivanoff, 2005), of all the external and internal signals only a few get access to it (Baars, 1997; James, 1890). In terms of cognitive economy, it is crucial to allocate these limited resources to cognitive processes that are worth. And within all of these processes, those gaining privileged access to consciousness are those that are more relevant and salient for human beings and the self (James, 1890). For example, sensory signals associated with emotional values or threats are unconsciously processed and prioritized into consciousness, as threat detection could be relevant for survival (Alpers & Gerdes, 2007; Öhman & Mineka, 2001; Tamietto & de Gelder, 2010; Vuilleumier & Driver, 2007). Furthermore, some aspects of social cognition can be processed without awareness, such as face perception, emotional expressions and gaze direction (for a review, see Axelrod et al., 2015), as humans are intrinsic social animals and social behavior is crucial. Some evidence showed that whereas consciousness is required for integrating novel information, previously learned associations are processed without conscious involvement (Mudrik et al., 2014).

Current models and theories of consciousness often overlook the role of the observer as the subject of conscious experience. Indeed, a fundamental aspect of consciousness is its intrinsic connection to the self, inherently tied to the 'I' of the subjective experience. This sense of self, and its relationship with the brain's representation of the body, is known as bodily self-consciousness (BSC). Thus, connecting the role of conscious and unconscious processing to the *Self* might be crucial for understanding self-consciousness (Damasio, 2012; Metzingher, 2004). The bodily self represents the physical substrate of one's existence, a spatial reference for moving and interacting within the environment. Monitoring or recognizing one's own body might become intrinsically important for survival and self-consciousness. For example, when an external object threatens the body, having a system that automatically reacts to such threats by having a fast sensory-to-motor bodily response

could be vital, without the need of the 'slower' and complex conscious response (LeDoux, 1998a). Within such a framework, it makes sense to postulate the presence of automatic brain mechanism that continuously track one's own body that might operate without awareness. We can nevertheless assume that the bodily self is the most relevant object in the environment, so one can expect that bodily-self signals can be prioritized into awareness (Van Der Hoort et al., 2017). Within this framework, BSC might reflect automatic brain processes, governed by bottom-up mechanisms that can arise unconsciously at a pre-reflective level. Thus, is it possible that some aspects of the bodily self might be processed without awareness? Such a view would be in line with Panksepp and Northoff' hierarchical model of the self, comprising the proto-self, core-self, and higher-order self-representations. In that framework, lower-order self-processing operates automatically and independently of conscious awareness. In contrast, higher-order self-processing, which involves cortical structures as well as frontal and temporoparietal regions, necessitates consciousness for the highest form of integrated and unified perception and experience (Panksepp & Northoff, 2009). To date, very little experimental attention has been paid to such a topic. In this thesis, I will try to explore the unconscious self and how the brain encodes bodily visual cues in relation to and in the absence of awareness.

1.2 *Aim and structure of the thesis*

The aim of this work relies on the investigation of how and which cues specifically related to the bodily self are processed before consciousness within two main research lines. Bodily-self processing, historically, has been studied through two main types of stimuli, namely faces and hands. Neuroimaging studies highlighted distinct and dissociable brain pathways and structures for faces (Kanwisher & Yovel, 2006) and bodily effectors (Peelen & Downing, 2007), suggesting that our brain considers the two classes of bodily stimuli as qualitatively different. In fact, whereas faces might represent key signatures of people's identities triggering appropriate social interactions, hands are

mostly related to environmental interactions. As for the *first research line*, the focus will be on hand stimuli. To my knowledge, there are no scientific studies on how the brain deals with its bodily effector before awareness. Thus, Chapter II will investigate how self-other distinction of bodily stimuli affects conscious access (Studies 1 & 2) and whether such mechanisms might produce a pre-reflective form of body ownership (Study 3). The *second research line* described in Chapter III will instead rely on face awareness. Faces represent a key feature of personal identity conveying a wide range of information such as age, sex, ethnicity, emotions, intentions and so on, being the most relevant stimuli for an intrinsically social animal as humans. Indeed, it's not surprising that faces are one of the most used stimuli to study the brain and also consciousness (Axelrod et al., 2015). However, only a few studies investigated how face identity could be processed in relation to visual awareness. This will be the focus of the second research line of this thesis (Chapter 3), in which we adopted an electrophysiological approach through the electroencephalogram (EEG) to investigate the effect of face identity on the EEG correlates of visual awareness (Study 4), and a neuropsychological approach to explore face familiarity processing in a single-case study involving patient MS, affected by hemianopia and prosopagnosia after a brain injury (Study 5). The general aim is to shed light on the interplay between the bodily self, identity processing and visual awareness.

1.3 *Main Methodologies for the study of visual awareness*

Unconscious processing can be explored within two main approaches (Chalmers, 1996; Searle, 2000): one follows the disruption of the content of consciousness through the degradation of sensory stimulus processing (sensory unawareness) or of attentional resources (attentional unawareness) (Tamietto & de Gelder, 2010), i.e., the local state; the second follows the disruption of the state of consciousness, such as during sleep or coma (Kouider & Faivre, 2017), i.e., the global state (Seth & Bayne, 2022). At the moment, the most influential way to explore the functions of unconscious processing relies on sensory unawareness, in which the stimulus strength is usually reduced to not

reach the threshold for conscious perception as assessed by different measures (i.e., subjective and objective measures; Kiefer & Kammer, 2024) and paradigms (e.g.: masking, attentional blink, rivalry; see Axelrod et al., 2015; Breitmeyer, 2015; Breitmeyer et al., 2015; Kim & Blake, 2005, for reviews of empirical methods for studying consciousness), each with pros and cons. Among those, interocular suppression paradigms (see **Fig. 1.2**), such as binocular rivalry, are the most used psychophysical techniques suitable for studying visual awareness. To briefly explain, binocular rivalry relies on the presentation of two different images, one for each eye, creating a conflict within monocular channels for conscious representation. Indeed, conscious perception do not unify the two images in a unique percept, but rather alternates back and forth the representation of the two images in a stochastic alternation cycle. The image that is temporarily perceived is said dominant, the other is said suppressed. Since Whiteston (1878) first experienced binocular rivalry (hereinafter, BR), vision scientists adopted such a paradigm to study which factors determine greater periods of 'dominance' in visual awareness of an image over the other, and what would be the faith of the image that is, at least temporary, 'suppressed' from consciousness, and what drives and resolves visual competition determining conscious representation. Different models explaining the rivalry phenomenon have been proposed, with the most prominent representing BR as governed by low and high multilevel mechanisms in which inhibitory and excitatory feedback connections of neuronal populations across the visual hierarchy interact in promoting or suppressing conflicting visual representations coming from the eyes (Hesse & Tsao, 2020; Lin & He, 2009; Sterzer et al., 2009; Tong et al., 2006). Furthermore, adaptation of the neuronal population representing the dominant stimulus influences its inhibitory strength to the suppressed stimulus, resulting in perceptual alternations (Alais, 2012; Alais et al., 2010; Blake et al., 2003; Kang & Blake, 2010; Levelt, 1965; Wilson, 2007). Stimuli that dominate perception for a longer time are believed to be consciously prioritized by the visual system (i.e., Alpers & Pauli, 2006), whereas those escaping suppression faster to gain dominance are thought to be unconsciously prioritized (i.e., Costello et al., 2009; Jiang et al., 2007). However, given the unpredictability and stochastic nature of the alternation cycle to precisely study and disentangle

conscious and unconscious processes, two variants of BR, namely the Continuous Flash Suppression (CFS; Tsuchiya & Koch, 2005) and its 'breaking' variant (bCFS; Jiang et al., 2007), have been developed to study visual processing in the suppression phase (Ciorli, et al., 2024; Gayet et al., 2014; Pournaghdali & Schwartz, 2020; Stein, Hebart, et al., 2011; Stein, 2019). In CFS, one eye is exposed to a high-contrast dynamic mask (typically updating at 10Hz of frequency) which completely suppresses the target image shown to the other, without the occurrence of perceptual alternations that characterize BR. This paradigm has proven to be extremely useful for controlling suppression times by prolonging the timing for unconscious stimulus processing. By progressively decreasing the visibility of the mask so that the target breaks the suppression, the "breaking" variant of the CFS allows to measure the timing stimuli needed to access visual awareness (see **Fig. 1.2** for a schematic representation of interocular suppression paradigms). The rationale underpinning the two BR variants is that CFS specifically disrupts conscious processing but, crucially, enables the information to be processed unconsciously. Thus, stimuli that are detected faster are thought to enjoy an unconscious prioritization mechanism that boosts the sensory signal into consciousness. Differences in detection times in bCFS have been taken as evidence that a wide range of higher-level cognitive processes can occur unconsciously (for a review, see Hassin, 2013): facial and bodily features (Ciorli & Pia, 2023; Lanfranco et al., 2023), semantic content (Costello et al., 2009; Jiang et al., 2007; Kerr et al., 2017; Yang & Yeh, 2011), emotions (Hedger et al., 2015; Vetter et al., 2019; Yang et al., 2007), degree of familiarity (Geng et al., 2012; Gobbini et al., 2013; Stein, End, et al., 2014; Stein et al., 2016), threat (Gayet et al., 2016), multisensory information (Aller et al., 2015; Zhou et al., 2010), food (Ciorli et al., 2024; Lee et al., 2022), and abstract concepts (Sklar et al., 2012).

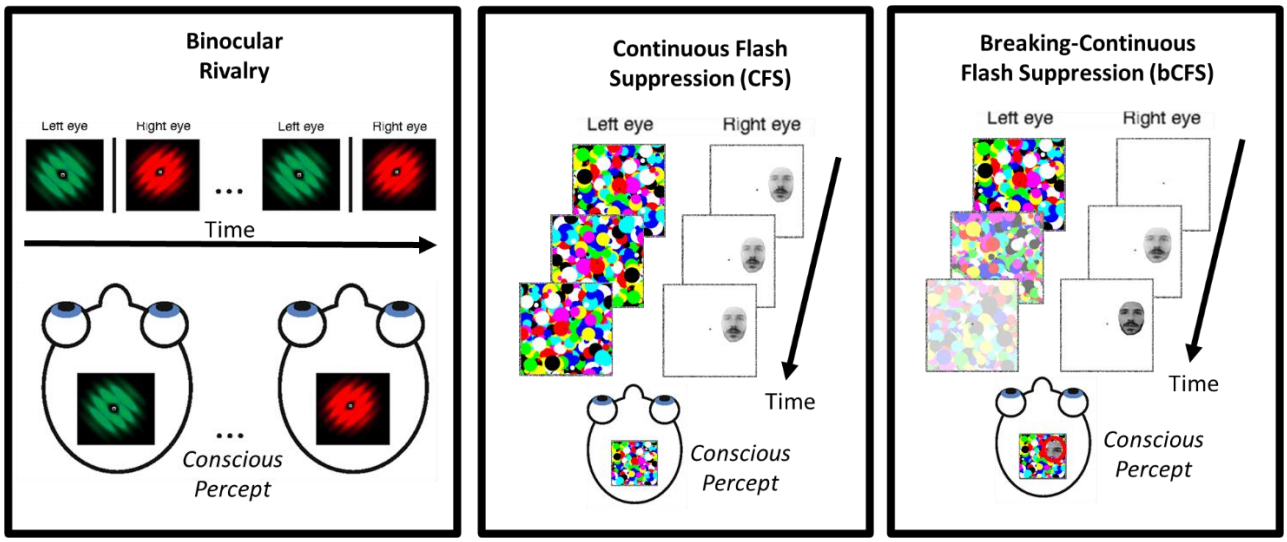

***Figure 1.2**: Representations of the three main interocular suppression paradigms, representing the time course of, respectively: Binocular Rivalry, for which within a continuous time the conscious percept alternates between the representation of the two images; Continuous Flash Suppression, for which a salient high-contrast mask shown to one eye efficiently suppresses a low-contrast target image shown to the other eye; the breaking-Continuous Flash Suppression paradigm, in which the target breaks the mask suppression after manipulating images contrasts (i.e., decreasing the mask one, while increasing the target's one).*

However, it is important to note that the bCFS paradigm relies entirely on a subjective response to stimulus visibility (namely, when it appears into consciousness), not entirely the best approach to demonstrate unconscious processing, for which a measure of stimulus awareness (with null sensitivity) must be contrasted with a measure of stimulus processing (showing some sensitivity) through a dissociative approach (Kouider & Dehaene, 2007; Schmidt & Vorberg, 2006). bCFS responses might be influenced by enhanced conscious processing or lower response criterion (Lanfranco et al., 2023; Stein, 2019), and it has been shown that it cannot provide unequivocal evidence for unconscious processing. Indeed, some of the above-mentioned findings have been attributed to confounds other than unconscious processing (i.e., Gray et al., 2013; Moors et al., 2016; Stein & Sterzer, 2012). Nevertheless, bCFS represents a unique paradigm to study the unconscious-to-conscious perceptual transition through a subjective measure, and recently novel paradigms to

control for conscious effects under interocular suppression have been proposed (Ciorli, Pia, et al., 2024; Coorey et al., 2023). On the other side, objective paradigms such as masking (Breitmeyer, 1984; Breitmeyer & Öğmen, 2007) are more suitable to the dissociative approach for demonstrating unconscious processing (Stein, 2019; Stein & Peelen, 2021). In backward masking (see **Fig. 1.3**), a stimulus is shown for a few milliseconds (i.e., 8, 17, 25, or 33ms), immediately followed by a mask that prevents conscious perception of the stimulus. Participants are often asked to provide a subjective measure of awareness, for example through the Perceptual Awareness Scale (Ramsøy & Overgaard, 2004), and to objectively discriminate or localize the target image. If the participant is shown to have a chance level performance on the discrimination task, objective unawareness of the critical stimulus dimension is provided (i.e., Stein & Peelen, 2021). Then, differences in indirect stimulus processing (i.e., localization tasks or brain activity) are genuinely related to unconscious processing, although the stimulus strength is reduced with respect to BR.

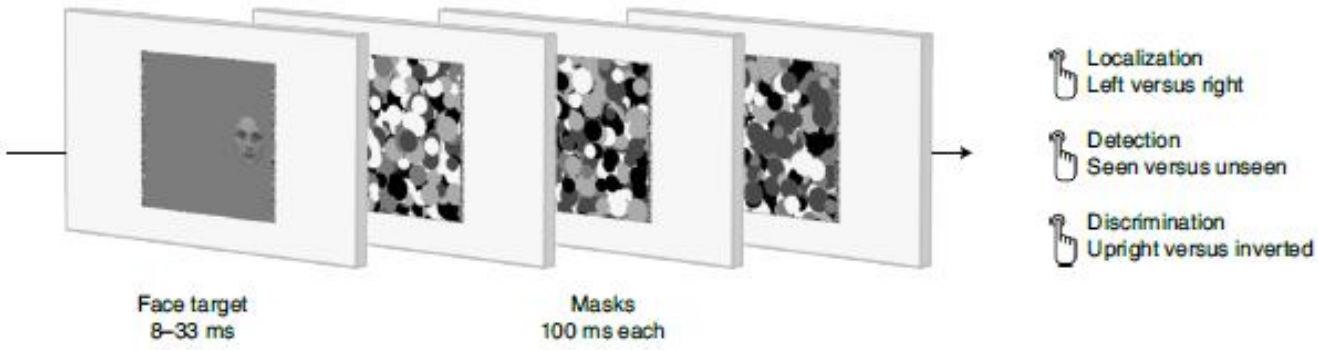

Figure 1.3: *This figure was taken from Stein and Peelen (2021). It shows an example of a backward masking trial, for which a target is shown for a variable timing (i.e., within the range of 8-33ms), followed by masks that prevents conscious stimulus processing. Then, participants are asked, within AFC accuracy-based tasks, to localize the stimulus position (i.e., stimulus processing measure), discriminate stimulus features (i.e., awareness of stimulus features), or to provide a subjective visibility measure (i.e., subjective awareness).*

In this work I took advantage of the interocular suppression paradigms to directly explore which identity-related bodily stimuli a) might enjoy preferential access to consciousness (bCFS; study 1, 2); b) entails behavioral effects while suppressed through CFS about one's body ownership (*Study 3*). In *Study 4*, backward masking was combined with the EEG for testing the effects of unconscious face identity processing in the electrophysiological correlates of visual awareness, whereas *Study 5* adopted a neuropsychological approach by studying unconscious face-familiarity processing in a patient affected by Hemianopia and Prosopagnosia.

Chapter II

On the relation between the Bodily-Self and Visual Awareness

'Consciousness science faces a unique problem. Unlike nearly all other scientific problems, the aim is not to explain a certain observable function but a first-person phenomenon'.

(Pinto & Stein, 2021)

2.1 *General Introduction*

The ability to distinguish between one's own body and the body of another person is a key signature of human nature, and necessary for survival. Indeed, the self-other distinction of corporeal stimuli is a prerequisite for a wide range of cognitive functions such as motor control, social perception, and interactions with others (Kaiser et al., 2008; Kessler & Thomson, 2010), necessary to actively move in the surrounding space. Such skill is known to rely on a complex interplay between a variety of sensorimotor signals, so that their optimal integration allows to successfully attribute a given bodily stimulus to the self or to another person. One key marker for BSC is a test for self-recognition, namely the marker test, postulating that if an animal can recognize the body as its own, he must have a self-concept and some levels self-consciousness. In this test, first developed by Gallup (Gallup, 1970), a colored mark is placed on a subject's face in a location that they cannot directly see, and then placed in front of a mirror. If the subject uses the mirror to inspect or touch the marked area, evidence of self-recognition is provided. Since Gallup's study, various species, including certain primates, elephants, dolphins, and magpies, have shown behaviors consistent with self-recognition in mirror tests (Plotnik et al., 2006; Prior et al., 2008; Reiss & Marino, 2001), while others typically do not pass the test. However, some animals might fail the test not due to a lack of self-awareness, but because mirrors do not play a significant role in their natural behaviors or due to differences in sensory

modalities. Recent studies proposed that self-recognition, arising around two years old in humans (Cebioğlu & Broesch, 2021; Lewis et al., 1985) might occur in various forms and that the mirror test may not capture all aspects of self-awareness (De Waal, 2019). Self-awareness can indeed be characterized by two different mechanisms: explicitly, which relies on the overt recognition of one's image, or implicitly, which relies on the covert prioritized processing of self-related stimuli (Ross et al., 1975).

Studies on bodily self-awareness in humans focusing on self-recognition typically involve the presentation of body parts as external objects that might belong to the self or to others separated from direct first-person experience (i.e., on a screen), and participants are asked to judge features that might change after experimental manipulations. The common result is that participants are found to be faster and more accurate in the processing of self-related, as compared to other-related, stimuli, a phenomenon named self-advantage or self-bias (i.e., Bortolon, 2018; Frassinetti et al., 2011; Ma & Han, 2010). Imaging studies showed that self-recognition engages a broad range of brain regions, from primary unisensory areas to higher-level multimodal association cortices (Devue & Brédart, 2011; Platek et al., 2004, 2008). Indeed, self-recognition is thought to arise from the ability to integrate self-related sensory information. Such multisensory integration is known also to produce the feeling of body ownership, which is the subjective experience that a body belongs inevitably to the self (Ehrsson, 2012; Tsakiris, 2017). In contrast to self-recognition studies which typically rely on implicit or explicit *judgments* of ownership, bodily illusions paradigms investigate the emergence of the subjective *feeling* that a certain object is part of one's own body schema (Tsakiris, 2010), as in the Rubber Hand Illusion or Full Body Illusion paradigms (Botvinick & Cohen, 1998; Maselli & Slater, 2013; see Study 3). At the neural level, brain imaging studies have shown that the premotor cortex, intraparietal sulcus, and extrastriate visual areas contribute to the experience of body ownership, while the temporoparietal cortex and insula are associated with first-person perspective experience (Ehrsson et al., 2004a; Ehrsson, 2012; Guterstam et al., 2013; Ionta et al., 2011, 2014; Limanowski et al., 2014; Petkova et al., 2011).

To date, there are no studies investigating how self-other distinction of bodily effectors, namely hand stimuli, is processed before awareness and which visual feature might be prioritized into consciousness. Moreover, whether such a possible unconscious mechanism supporting self-other distinction might also trigger body ownership at a preconscious level is unknown. The aim of the following studies is to evaluate how the most important cues for bodily effectors subserving self-other distinction (Study 1 & 2) and body-ownership (Study 3) act with respect to visual awareness.

2.2 Study 1: **Spatial Perspective and Identity in Visual Awareness of the bodily self-other distinction**

From: Ciorli & Pia (2023), Scientific Reports

https://doi.org/10.1038/s41598-023-42107-z

2.2.1 *Introduction*

Extracting relevant visual information from human bodies allows us to build a variety of important judgments as, for instance, those related to age, ethnicity, gender, and so on. Among these, there is also the ability to attribute the seen body/body parts as belonging to oneself or to another person. Within an experimental context, one way to scientifically investigate the self-other distinction for corporeal stimuli in visual modality is by manipulating the spatial perspective in which the stimulus appears. The rationale behind this idea is that a human body part, the hand for instance, can potentially be perceived from a first-person perspective (i.e., upright orientation with fingers up), or in a third-person perspective (i.e., upside down orientation, with fingers downward). Within this framework, it has been demonstrated that hand images depicted in the first-person perspective are naturally attributed to one's own body, whereas those in the third-person perspective are referred to the body of someone else (Brady et al., 2011; Conson et al., 2010; Choisdealbha et al., 2011). Interestingly, a number of neuroimaging studies reported different patterns of cortical activation that underlie the visual processing of hand stimuli coded in the two perspectives (Carey et al., 2019; Chan et al., 2004; Saxe, Jamal, et al., 2006). This, in turn, suggests a possible functional dissociation between the two perspectives. A second option to examine the self-other distinction for visually presented hands is, much more obviously, to vary the identity of the stimulus that, according to its peculiar visual features, is attributed to oneself or another person. Within this other line of research, it has been shown that the encoding of one's own hand with respect to the one of another person is

underpinned by substantially different patterns of brain activity (De Bellis et al., 2017; Hodzic, Kaas, et al., 2009; Hodzic, Muckli, et al., 2009; Myers & Sowden, 2008), and they can be selectively disrupted employing experimentally controlled virtual lesions (Pann et al., 2021; Urgesi et al., 2007). Within a neuropsychological approach, it has been reported that brain lesions to the right hemisphere can disrupt the so-called self-advantage (i.e., the facilitation to implicitly discriminate *self*-versus other people's visually presented hands (Frassinetti et al., 2008, 2011). Moreover, brain damage can lead to the misattribution of the own contralesional limb to another person (Romano et al., 2014; Vallar & Ronchi, 2009), or even the opposite behavior, namely the misattribution of somebody else's arms to oneself (Candini et al., 2022; Fossataro et al., 2018; Garbarini et al., 2013). As above, also these data suggest that the stimulus identity (i.e., self or other) might be functionally dissociable.

The abovementioned considerations identify spatial perspective and identity as the two crucial cues to successfully assigning a seen hand to the own body or the body of somebody else. However, how these two features differentially affect the information flow from early levels of unconscious visual processing to a complex conscious representation of the self-other distinction is largely unknown. Given the innate social attitude of the human species, understanding whether these cues can influence self-other distinction even unconsciously, or rather, whether they necessarily require visual awareness is a fundamental scientific challenge. Moreover, to the best of our knowledge, there is only one published study that addressed the relation between visual awareness and self-other distinction (Van Der Hoort et al., 2017). That work reported that multisensory integration subserving the attribution of the own body parts to the self actually promoted visual awareness. To fill this gap, here we focused on the role of perspective and identity in the prioritization of hand stimuli in visual awareness. As regards the access to visual awareness, we employed the breaking-Continuous Flash Suppression paradigm (bCFS). Here, a high-contrast dynamic mask flashed to one eye effectively suppresses a target stimulus of increasing intensity presented to the other eye. By decreasing the contrast of the mask over the trial, the suppressed stimulus becomes visible and the time required to detect it reflects the moment in which it gains access to awareness (Jiang et al., 2007; Stein, Hebart,

et al., 2011; Stein, 2019). In summary, in the present study we compared self-hand stimuli vs. other-hand stimuli presented in first-person perspective vs. third-person perspective, and we measured the time of access into awareness of such stimuli In line with the literature suggesting possible functional dissociations between perspective and identity, we predicted that they could be differentially prioritized in visual awareness.

2.2.2 *Methods*

Participants

22 (15 F, mean age = 24.5 ± 2.5 years) participants with normal or corrected-to-normal vision were administered the experiment after having provided a written informed consent. Since previous work showed that participants are advantaged in the processing of the dominant self-hand (Conson et al., 2010), we recruited both right-handed (19) and left-handed (3) participants (self-report). They were all naïve to the research questions underneath the study, which was approved by the Ethical Committee of the University of Turin (protocol n. 0486683) and performed in following relevant guidelines of the declaration of Helsinki. Initial sample size (n = 27) was based on similar studies using such paradigms (i.e., Weng et al., 2019), and we later estimated the statistical power of our results in a post-hoc power analysis with g*Power (3.1.9.7).

Apparatus, stimuli, and procedure

At the arrival, each participant's dominant hand was photographed with a digital camera in a controlled setting. The picture was taken from above in the first-person perspective. Then it was black-and-white transformed, cropped with Photoshop (2019), and a 180°-rotated copy was created. A same-laterality and same-gender hand from the previous participant was used as 'other' stimulus and shown in advance for visual familiarity acquisition. Thus, the target stimuli were self/other hands in first/third-person perspective (2 x 2 design).

The experiment was programmed with MATLAB (Release 2021b) and Psychtoolbox, and 3° x 4.2° target stimuli were presented on a BenQ Monitor (1.920 x 1.080-pixel resolution, 120 Hz, 24") at a distance of 57 cm. Participant's head was stabilized by a chinrest with a custom built-in stereoscope, allowing for stable binocular vision once adjusted for each participant. The target stimulus was presented to one eye and a dynamic high-contrast Mondrian-pattern mask (i.e., randomly arranged circles of distinct colors, and sizes between 0.3 and 1.2°) was flashed at 10Hz to the other. Both the stimulus and the mask were contained in a fusion square (11.7° x 11.7°, one per eye, each at a distance of 5.8° from the center) made of noise-pixels (width .2°). The screen background was black, while the fusion squares' area was white with a black fixation cross in the center. For each trial, the target stimulus was shown by linearly decreasing its transparency from 100% to 0% within the first second of each trial, presenting it at the top or the bottom of the fusion square (with a random horizontal jitter). At the same time, the transparency of the high-contrast mask presented to the other eye was linearly increased from 0% to 100% within 7 seconds (starting after the first second of the trial). Instructions were presented in a written and verbal form, and 8 practice trials were employed to familiarize with the task. Participants were asked to respond as fast and accurately as possible by localizing the position of the target through the keyboard arrows (i.e., top position: up arrow key, bottom position: down arrow key), once visible. They were also required to answer even if they simply had a strong feeling that something more than the mask was present (i.e., preventing conscious perception of stimuli). During each trial (lasting until response or for a maximum of 8 seconds), they were asked to keep the eyes on the central fixation cross, to avoid active gaze-searching, to prevent both blinking and closing one eye at a time (which were allowed in the 1 second ITI). Within each of the four conditions, stimuli were randomly administered 24 times to the right eye in a top position, 24 times to the right eye in a bottom position, 24 times to the left eye in a top position, and 24 times to the left eye in a bottom position for a total of 96 trials. The four conditions were administered to each participant in a randomized order for a total of 384 trials. After 128 and 256 trials, a small break was made (see **Fig. 2.1** for the time course of a trial and stimuli).

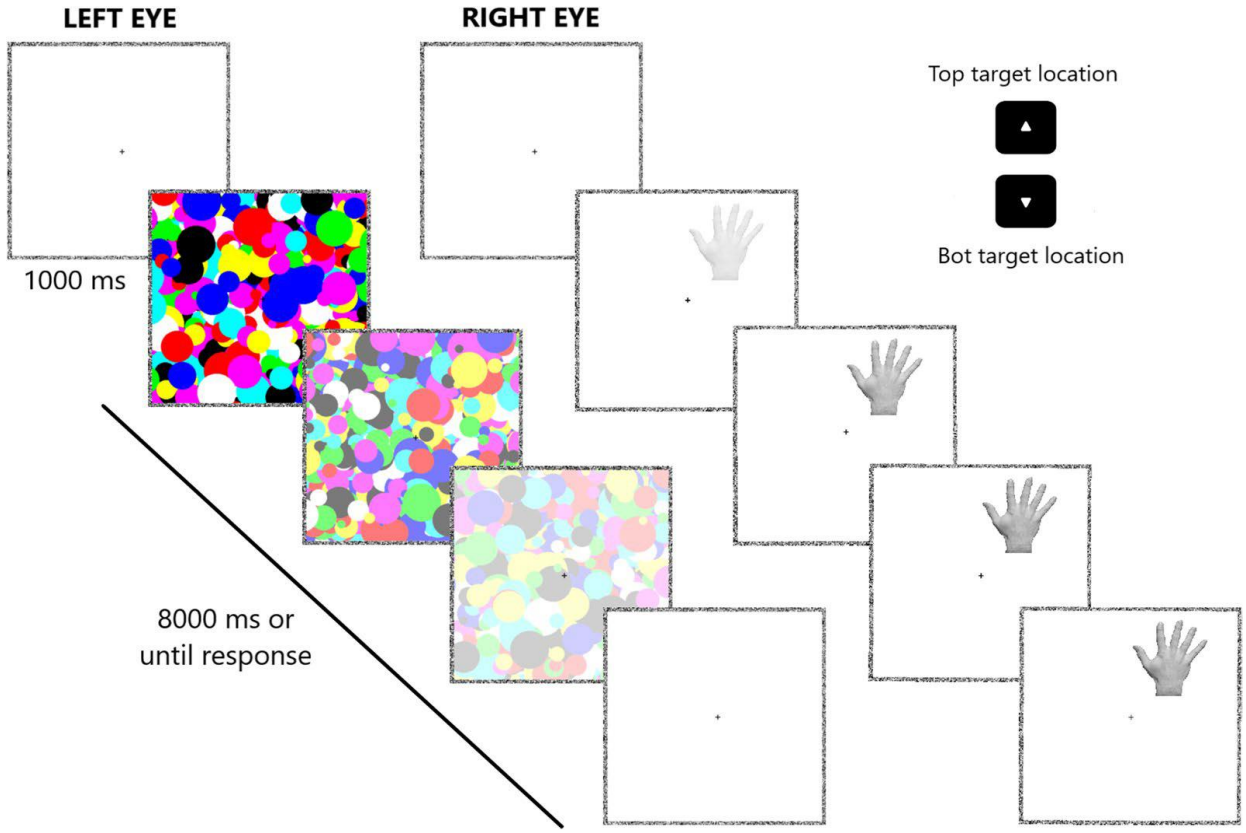

Figure 2.1*: Schematic representation of the bCFS trial. After 1 s of ITI, a high-contrast mask updating at a frequency of 10 Hz is shown to one eye, and its transparency was increased from 0 to 100% within 1-7 s after the ITI end. The target hand is shown to the other eye, and its transparency was decreased from 100 to 0% within the first second of the trial. Participants had to detect the target location once the target appeared as fast as possible.*

Statistical analysis

Participants reporting unstable binocular perception (N = 0), those with accuracy lower than 90% (N = 4), and those with a mean value ± 2.5 SD from the group mean (N = 1) were excluded, so that the final sample consisted of 22 participants. Trials with response time lower than 300ms (.35% of the trials) were excluded since they indicated that stimuli were not suppressed. Then, for each of the four conditions, mean response times for corrected responses only were calculated, and then log-transformed to account for a not normal distribution of the data (Shapiro Wilks < .05). We reported

both frequentist statistics and Bayes factors (BFs; Cauchy distribution = .707) by using JASP (JASP Team, 2016). We conducted a 2 x 2 repeated-measures ANOVA with the factors Identity (self/other) and Perspective (first/third). For significant effects, we assessed to what extent the evidence supported the alternative hypothesis model (BF_{10}). For non-significant results, we assessed to what extent the evidence supported the null hypothesis model (BF_{01}).

2.2.3 *Results*

Mean response times for correct response before the log-transformation were 2.49 s (SE = ± .17) in the *self/first-person* condition, 2.71 s (SE = ± .18) in the *self/third-person* condition, 2.50 s (SE = ± .18) in the *other first-person* condition, and 2.75 s (SE = ± .19) in the *other third-person* condition. The repeated-measures ANOVA on log-transformed means for correct responses revealed a main effect of perspective ($F_{(1,21)} = 17.49$, $p < .001$, $\eta_p^2 = .454$; $BF_{10} = 74.27$), with significantly ($t = -4.182$, $p < .001$, Cohen's d = -.89; $BF_{10} = 76.61$, very strong evidence in favor of the alternative hypothesis) faster responses to *first* (mean = .29, SE = ± .031), than *third* (mean = .33, SE = ± .032) *person* perspectives (see **Fig. 2.2**). The main factor identity ($p = .53$; $BF_{01} > 100$, very strong evidence for the null hypothesis) and the interaction perspective x identity ($p = .59$; $BF_{01} = 8.70$) were not significant. See Figure 2 for the results. We then performed a post-hoc power analysis, revealing that we had the 99% of statistical power to detect the effect of perspective in a two-tail t-test with our sample size, alpha (.05), and effect-size ($d = 1.2$) determined by their mean values and standard deviations.

Summarizing, these results show that first-person, with respect to the third-person spatial perspective, speeded up the access to visual awareness for hands stimuli.

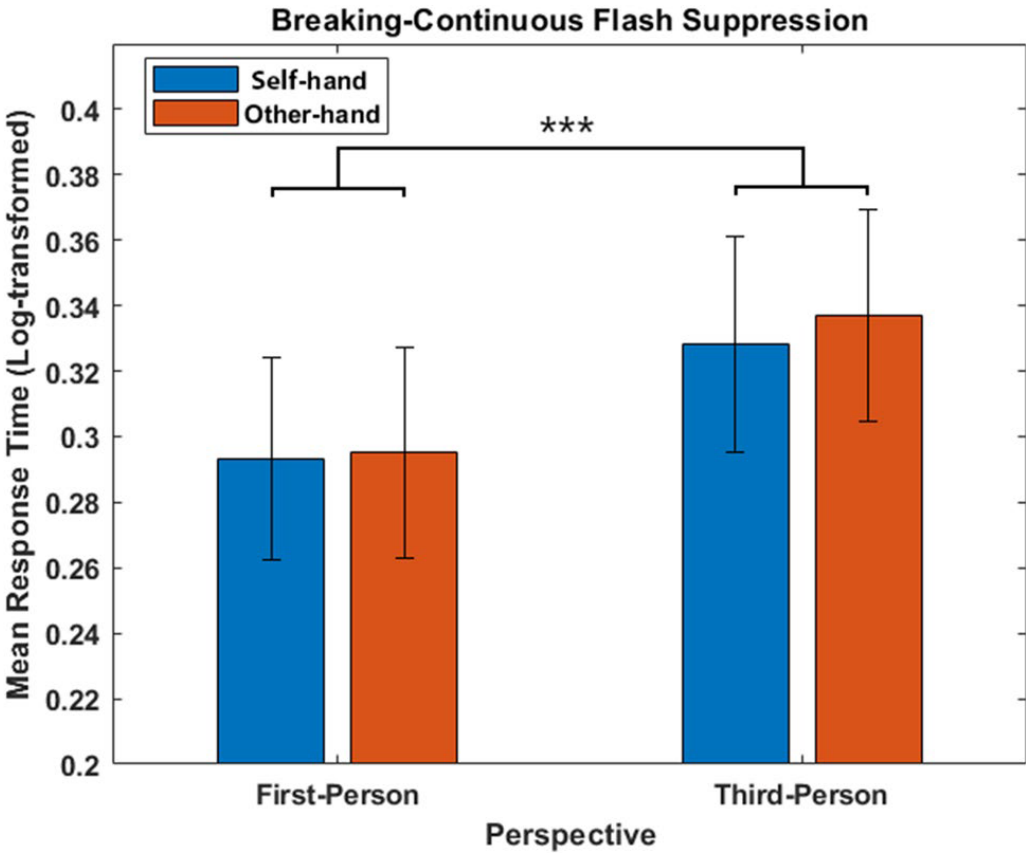

***Figure 2.2**: Mean log-transformed response times as a function of hand-perspective and identity (and SE), reflecting target's suppression times. *p < .05, **p < .01, ***p < .001*

2.2.4 *Discussion*

In the present study, we investigated the role of spatial perspective and identity in the emergence into visual awareness of the self-other distinction for bodily stimuli (i.e., hands). We capitalized on stimulus prioritization by focusing on the time of access through the breaking-Continuous Flash Suppression paradigm. We compared self-hand stimuli vs. other-hand stimuli presented in the first-person perspective vs. third-person perspective. Our results show that only spatial perspective promoted the stimuli in visual awareness. Specifically, the visual image of a hand presented in the first-person perspective broke the suppression faster than the same visual image, with identical low-level features, presented in the third-person, regardless of its identity. In other words, the hand's perspective was differentially processed before entering consciousness, with the first-person perspective being prioritized. How can we explain this result? Firstly, the effect of visual perspective

per se is not trivial but, rather, consistent with a number of studies with the same paradigm suggesting that not only low-level, but also high-level stimulus properties can be processed before consciousness (i.e., something typically thought not to be possible without awareness; see Hassin, 2013; Hesselmann & Moors, 2015; Pournaghdali & Schwartz, 2020 for discussions on this topic). For instance, it has been demonstrated that face orientation (e.g., Ciorli et al., 2024; Jiang et al., 2007; Stein et al., 2011, 2016), facial emotional content (e.g., Capitão et al., 2014; Yang et al., 2007; Zhan et al., 2015), eye gaze direction (Lanfranco et al., 2022; Stein et al., 2011), familiarity and emotional valence of words (Geng et al., 2012; Gobbini et al., 2013; Yang & Yeh, 2011), multimodal congruency (Zhou et al., 2010), and degree of natural content of the visual scene (Mudrik et al., 2011) can modulate the suppression time. Some of these high-level effects have been replicated also with more objective and accuracy-based techniques (e.g., face orientation, Stein & Peelen, 2021; and eye gaze direction, Lanfranco et al., 2022). However, others were not, being confounded by differences in low-level features (Gray et al., 2013; Stein & Sterzer, 2012), decision criteria (Lanfranco et al., 2020), and object-scene integration (Biderman & Mudrik, 2018; Moors et al., 2016), highlighting how such factors might impact on conscious access measures misinterpreting the scopes and the limits of unconscious perception (Stein, 2019). But what about the interpretation of the specific access to awareness advantage of the first-, with respect to the third-person perspective that we reported here? One of the already mentioned neuroimaging studies (Chan et al., 2004) manipulated both the visual perspective and identity of human body images. Among the various patterns of brain activations, the work reported that a specific brain structure (i.e., the left Superior Parietal Lobule SPL) was significantly more activated in first-, than in third-person perspective. Interestingly, other studies investigating the neural correlates of representing the environment from egocentric perspectives in a broader sense reported the same selective activation (Leplaideur et al., 2021; Lester & Dassonville, 2014; Schindler & Bartels, 2013). Such set of evidence seems to be in line with the known role of the SPL in representing nearby stimuli in body-centered coordinates (Colby & Goldberg, 1999). Importantly, these representations in SPL are thought to be largely unconscious (Gray, 2004) because

of their roles that mostly deal with visuomotor control of actions. In other words, such unconscious nature guarantees a quick integration of visual corporeal inputs over eye fixations. This, in turn, would allow the generation of stable visuospatial representation of the own body regardless of the ongoing saccades and attentional focus. According to all these considerations, here we put forward the idea that our findings might represent the behavioral counterpart of such unconscious processing of egocentric body representations. Such a direct body coding, without a continuous update of the eye position, could be further optimized if irrelevant information is suppressed. Hence, the absence of any identity effect that we report here could simply reflect an optimization procedure. Interestingly, in their paper, Chan and colleagues (2004) examined also the role of identity of bodily stimuli (i.e., self vs other) and did not find any differential activation at the level of the SPL. Such hypothesis is further supported by studies showing that the dorsal pathway is less affected by awareness manipulations (Fang & He, 2005; Hesselmann, 2013; Lin & He, 2009; Ludwig et al., 2016; Ludwig & Hesselmann, 2015; Zhan et al., 2018).

Summarizing, here we demonstrated that spatial perspective, but not identity, differentially affected visual awareness prioritization, with an unconscious advantage for the first. Capitalizing on the existing literature, we argue that unconscious prioritization of the first-person perspective would represent at the behavioral level a mechanism that supports action monitoring through the generation of a stable visuospatial body representation. Moreover, this process would be optimized by suppressing irrelevant information such as, for instance, stimulus identity. These considerations indicate that the self-other distinction for visually presented bodily stimuli seems to be strongly rooted in the interplay between spatial perspectives displaying a prioritization before conscious perception. Those cues can be sufficient in a large variety of daily life situations, so that identity would be involved only when strictly necessary, perhaps at more post-perceptual and higher cognitive levels. Interestingly, such suppression of identity features is also adaptive, in a way that perceptual hand features might change (i.e., while wearing gloves), but the perspective in which you perceive yourself or another person remains stable. Interestingly, this is in line with the literature on bodily illusions

based on multisensory integration. These experimental manipulations show that external objects as, for instance, rubber hands (Botvinick & Cohen, 1998; Burin et al., 2018; Costantini & Haggard, 2007a; Pia et al., 2013) or virtual bodies (Maselli & Slater, 2013; Petkova & Ehrsson, 2008; Pyasik et al., 2022), can be misattributed to oneself. Crucially, this illusory experience occurs if bodily stimuli are presented in the first-, but not in the third-person perspective, and this happens regardless of its visual appearance (see *Study 3*).

Before concluding, we must acknowledge some limitations, as well as future directions for novel studies. The first possible problem regards the fact that low-level features, known to have a vital role in unconscious processing, could have had an impact on our results. However, we believe this is unlikely since, apart from the fact that the stimuli creation was performed under rigorous experimental rules, low-level features were identical for the two spatial perspectives, being the same stimulus rotated by 180 degrees, and self-hand stimuli were used as other-hand stimuli for the subsequent participant (i.e., we alternated the same stimuli, keeping the same low-level features and only changing their high-level meaning in the eye of the observers). A second possible limitation is related to the so-called inversion effect reported for faces and bodies (Yovel & Kanwisher, 2005). This effect consists in the reduced ability to visually recognize an object shown upside-down since that object entails an intrinsic canonical orientation. However, hands do not seem to have such a default representation (i.e., we are visually familiar with upside-down hands representing others). A third problem is the fact that bCFS is known to have intrinsic limitations for studying objective unconscious processing (Hesselmann, 2019). Hence, more stringent techniques (e.g., dissociation paradigms; Stein & Peelen, 2021) should be employed to overcome these limitations by disentangling the role of response bias from detection sensitivity, which might had a role in our experiment, in order to test whether such effects survive in conditions of objective unawareness.

2.2.5 *Interim Conclusions*

Study 1 demonstrated that spatial perspective, but not identity, differentially affects visual awareness prioritization, with an unconscious advantage for the first-person perspective. We argued that unconscious prioritization of the first-person perspective would represent at the behavioral level a mechanism that supports action monitoring through the generation of a stable visuospatial body representation. Moreover, this process would be optimized by suppressing irrelevant information such as, for instance, stimulus identity. Those cues can be sufficient in a large variety of daily life situations, so that identity would be involved only when strictly necessary, perhaps at more post-perceptual and higher cognitive levels.

Whereas our findings suggest that hand visual appearance does not affect conscious access, others reported a self-advantage in an implicit self-other discrimination of hand stimuli (Frassinetti et al., 2008, 2011). In the next study, we attempted to clarify at which stage and to which extent visual identity features might interact with visual awareness in a top-down fashion, rather than as a bottom-up sensory processing (Apps & Tsakiris, 2014).

2.3 Study 2: **The role of identity Priming on the (unconscious) bodily-self Attribution**

From: Ciorli and Pia (2024), Psychological Research

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2.3.1 *Introduction*

Crucially for the purpose of the present study, in *Study 1* (Ciorli & Pia, 2023) we speculated that the lack of any identity effect on the conscious access of hand stimuli resulted because such feature relies on different or/and higher processes not indexed by our paradigm. Interestingly, this idea is in line with bodily illusions literature showing that external objects (e.g., fake hands; Burin et al., 2018; Costantini & Haggard, 2007; Pia et al., 2013, or virtual bodies; Maselli & Slater, 2013; Petkova & Ehrsson, 2008; Pyasik et al., 2022) are misattributed to the self if bodily stimuli are presented in a first- (not in the third-) person perspective, but regardless its visual appearance (i.e., identity). It is worth of noticing, however, that the absence of evidence is not the evidence of absence (Altman & Bland, 1995). Indeed, other studies demonstrated that humans are more accurate in implicitly recognizing the own hand with respect to somebody else's hand (Frassinetti et al., 2011), although on a completely different paradigm, without disambiguating the role of visual processing on the self-hand advantage.

According to the above-mentioned considerations, here we further investigated the role of identity on the self-other distinction. To do so, we capitalized on the phenomenon of priming, that is the improvement in accuracy or speed responses to stimuli when they are preceded by a related stimulus that pre-activates associated information (Maljkovic & Nakayama, 1994). Specifically, we investigated the role of top-down identity context on the conscious access of hand stimuli belonging to the participant or to another person, presented in a first- or third-person perspective. The bCFS is a suitable paradigm for testing also the influence of contextual factors in the timing for visual

awareness of invisible stimuli (Gayet et al., 2014). Indeed, it has been demonstrated a faster conscious access of stimuli when preceded by consciously perceived congruent primes at multiple levels, such as semantic (Costello et al., 2009), multimodal (Alsius & Munhall, 2013), and memory (Gayet et al., 2013; but see Stein et al., 2023) processing. In line with these considerations, we designed a bCFS experiment in which each trial was preceded by an identity-related prime (i.e., self/other faces) to test whether activating the self/other representation in a top-down fashion would have influenced spatial perspective and identity cues to change the time for visual awareness of hand stimuli. Congruently with the fact that top-down context plays a role in self-recognition, self-other distinction (Apps & Tsakiris, 2014), and conscious perception (Gilbert & Li, 2013; Hohwy & Seth, 2020), we hypothesized that face primes would prioritize the breaking of congruent hand stimuli in visual awareness, whereas conscious access would be slower for incongruent conditions.

2.3.2 *Methods*

Participants

Twenty-six (eighteen females, mean age = 23 ± 3 years) right or left-handed (n = 2) participants (self-report) with normal or corrected-to-normal vision participated in the study approved by the local ethical committee (protocol n. 0486683). Sample size was decided according to a published study with the same paradigm and similar design (i.e., Costello et al., 2009). We nevertheless computed achieved statistical power in a post-hoc power analysis with g*Power.

Apparatus, stimuli, and procedure

Participant's dominant hand (target stimulus) was photographed in a first-person in a laboratory setting, together with a photo of their own face (prime stimulus). The hand picture was black-and-white transformed, and cropped, and a 180° rotated copy was created. As with other stimuli, a same-gender face and same-laterality hand from the previous participant were employed

(and presented in advance for familiarization). Thus, the target stimuli were the self or other hands presented in first or third-person perspective, and prime stimuli were the self or other faces (2 x 2 x 2 design). MATLAB (2021b) and Psychtoolbox were used for programming, and 3° x 4.2° target stimuli were presented on a BenQ Monitor (1.920 x 1.080-pixel resolution, 120 Hz, 24") at a distance of 57 cm. The head of the participants was stabilized by a chinrest with a custom built-in stereoscope able to guarantee stable binocular vision after ad hoc adjustments. Before each trial, participants were consciously exposed to the prime face (500ms) representing the participants' own face or a stranger same-gender face, binocularly in the two fusion squares (11.7° x 11.7°). Primes were not related to the bCFS task, but participants were asked to keep in mind the face while localizing the suppressed target hand, as sometimes they could have been asked to select the correct prime that preceded the trial (each then shown for 500ms, divided by 650ms). Prime-check trials consisted of 12.5% of the total trials (forty-eight) and were included in the experiment to enhance the effect of the primes and induce the participant to pay attention to them. Following the prime, the same bCFS trial structure as in *Study* 1 was adopted. The total experiment consisted of 384 trials (counterbalancing target-eye presentation, target position, target identity and primes) divided into 3 blocks. After 128 and 256 trials, a small break was made (see **Fig. 2.3** for time course of a trial).

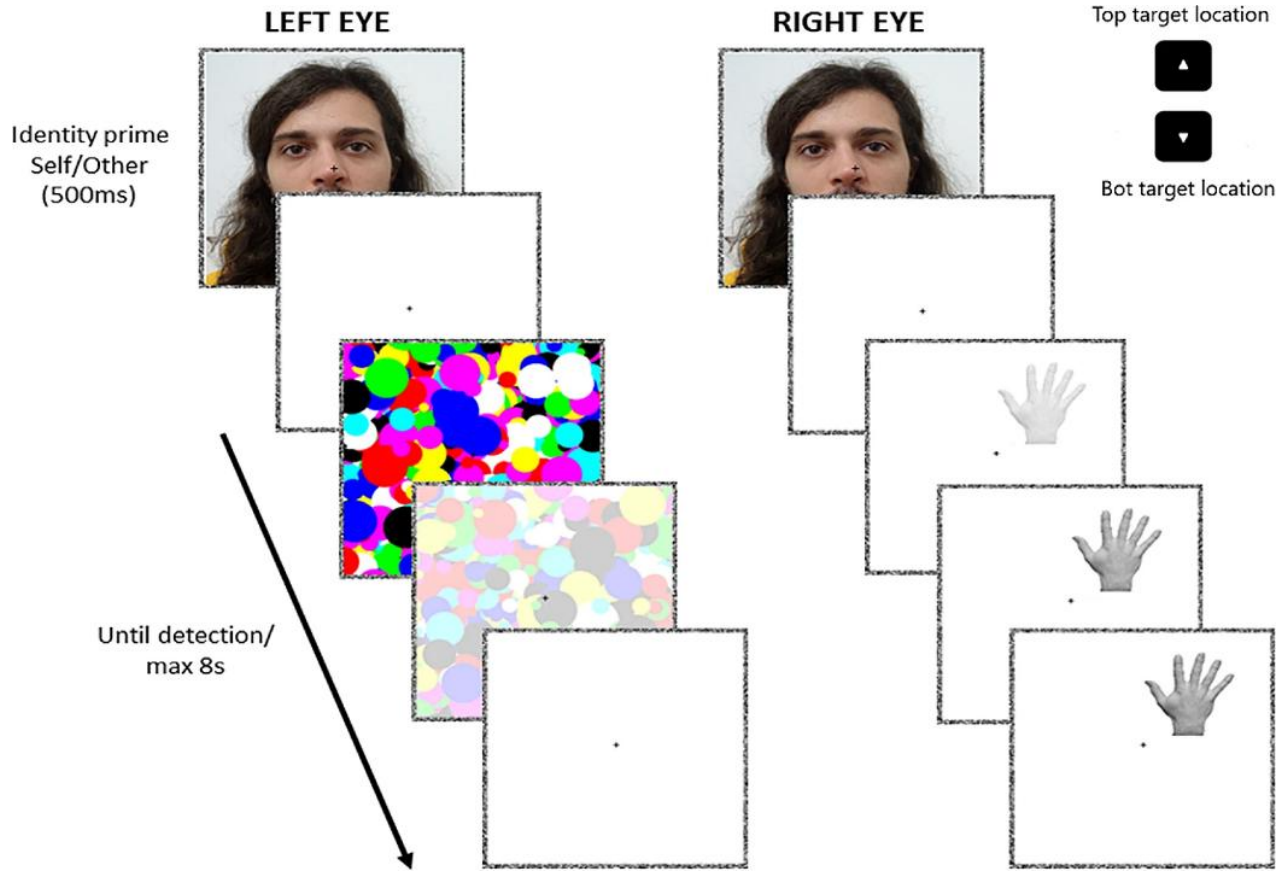

Figure 2.3*: The trial started with 500ms of binocular prime presentation (self/other face). Then, a dynamic Mondrian pattern is shown to one eye, being fully visible for 1 s and then linearly decreasing its contrast from 100 to 0% within 7s. At the same time, the target hand is shown to the other eye, being initially invisible but linearly increasing its visibility to 100% in 1 s. Each trial lasted for a maximum of 8.5 s or until subject detection response.*

Statistical Analysis

No participants reported either instable binocular perception or a prime-check accuracy lower than 75% (i.e., no attention to primes), whereas one was excluded because of an accuracy lower than 90%, as a widespread practice in bCFS studies. The final sample consisted of twenty-six participants. Trials with a response time lower than 300ms (3.9% of the trials) were excluded since they indicated that stimuli were not suppressed. Then, for each of the eight conditions, mean response times for corrected responses only were calculated, and then log-transformed because of a not normal data distribution (Shapiro-Wilk < .05). A repeated measure ANOVA with the factors Prime (self/other-

face), Identity (self/other hand) and Perspective (first-/third-person) was run with JASP (JASP Team, 2016). Then, in order to further analyze our data, we run two separate repeated measures ANOVA for each perspective with the factors Prime (self/other-face) and Identity (self/other hand).

2.3.3 *Results*

Mean accuracy for the localization task was .96, while mean prime-check accuracy was .96. Mean response times for correct response before the log-transformation were 1.57 s (SE = ± .13). The 2 x 2 x 2 repeated measure ANOVA revealed a main effect of perspective ($F_{(1,25)} = 22.06$, $p < .001$, $\eta_p^2 = .468$), with significantly ($t_{(25)} = -4.65$, $p < .001$, Cohen's d = .24) faster responses to first ($mean_{(log)} = .09$, SE = ± .03), than third ($mean_{(log)} = .13$, SE = ± .03) person perspective (see Figure 2). Moreover, a triple interaction between Prime x Identity x Perspective was found ($F_{(1,25)} = 5.71$, $p < .05$, $\eta_p^2 = .186$). As regards the two separate repeated measures ANOVA, we found within the First-Person perspective, a significant interaction ($F_{(1,25)} = 6.64$, $p < .05$, $\eta_p^2 = .210$) with slower response to other-hands primed with other faces as compared to all the other conditions, namely other-hands primed with the self-face ($t_{(25)} = 3.01$, $p < .01$, Cohen's d = .59), self-hands primed with other face ($t_{(25)} = 2.13$, $p < .05$, Cohen's d = .49), and self-hand primed with self-face ($t_{(25)} = 2.11$, $p < .05$, Cohen's d = .41). None of the main factors (i.e., Prime and Identity) were significant ($p > .05$). The same analysis on the Third-Person perspective condition yielded no significant effects ($p > .05$). See **Figure 2.4**. A post-hoc power analysis (performed with g*Power) revealed that with our sample size, we had 99% of statistical power to detect the effect sizes of our significant effects (perspective and interactions).

Summarizing, these results show that first-, with respect to the third-, person perspective broke the suppression faster. Moreover, in the first-person perspective other-hands stimuli preceded by other-face prime broke the suppression slower with respect to other-hands stimuli preceded by other-face prime, and to self-hands stimuli preceded by self- or other- face prime.

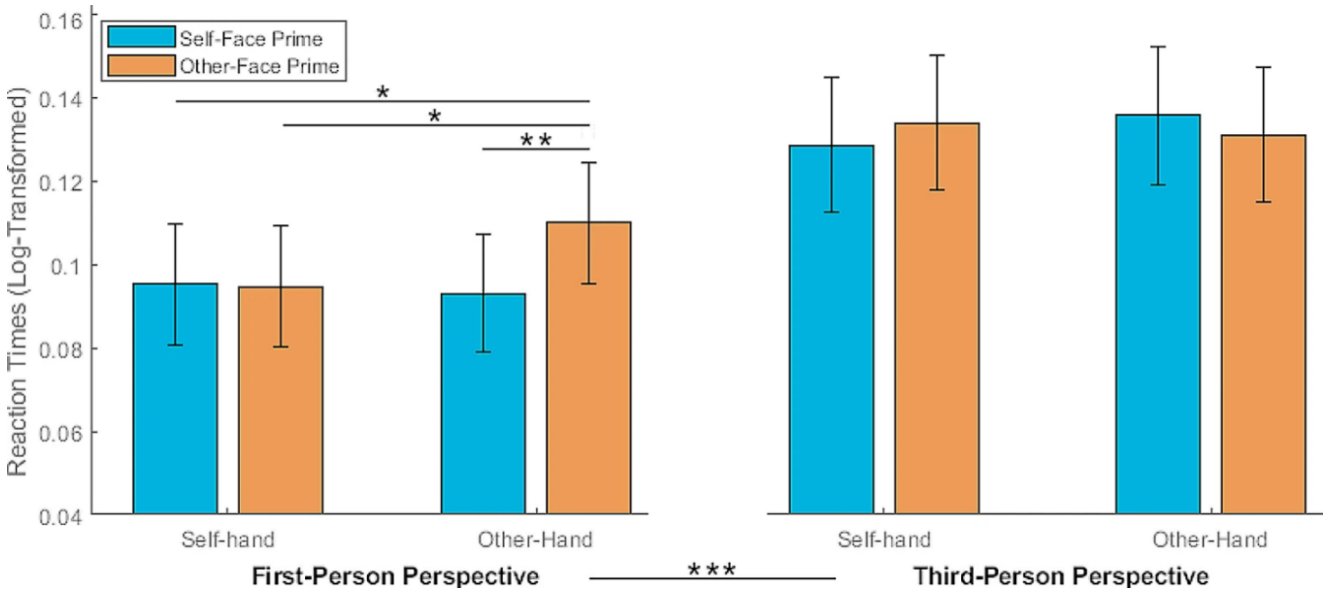

Figure 2.4*: On the left, mean log-transformed response times for First-Person perspective as a function of hand identity and prime face (with SE), indicating target's suppression times. On the right the same indices but within the Third-Person perspective. *p < .05, **p < .01*

2.3.4 *Discussion*

By means of the breaking-Continuous Flash Suppression paradigm and priming, we investigated whether and to which extent conscious identity primes acted upon perspective and identity cues changing the timing of the access to awareness of hand stimuli. We found that the first-, as compared to the third-person, speeded up the response but, crucially, we also reported that in first-person perspective other-hands stimuli preceded by other-face priming slowed down the response concerning all the other conditions.

As regards the first-person perspective unconscious advantage, we replicated the results of *Study* 1: the perspective from which one's own body is typically seen is privileged before awareness. We interpreted the datum as a prioritization of an egocentric body coding fundamental to support action monitoring. We also argued in favor of the absence of any identity effect (i.e., self or other) of the stimuli at the unconscious level (claiming that these features would be relevant at more post-perceptual and higher cognitive levels). The idea was that an efficient visuomotor control process

(i.e., quick motor adjustments) must suppress irrelevant information as the identity of the stimulus. However, in the present study, we also found an interaction between priming and the other two variables (i.e., perspective and identity) so that adding an identity context through conscious identity-related primes (i.e., faces) activated unconscious identity processing in first-person perspective only. Specifically, in such a perspective, *other-hands* stimuli preceded by *other-face* priming slowed down the responses with respect to other-hands stimuli preceded by self-face priming, and to self-hands stimuli preceded by self- or other-face priming. In the rest of the discussion, we will try to explain these results.

Recently, it has been proposed to extend the predictive coding theories of human brain functioning (Friston et al., 2006) to self-recognition (Apps & Tsakiris, 2014; Tsakiris, 2017) and the construction of visual awareness (Hohwy et al., 2008). Within this framework, the own body would emerge as a probabilistic representation (i.e., the most likely to be 'me' object) from the interplay between body priors and actual incoming body-related sensory signals. Specifically, priors trigger predictions about the sensory consequences evoked on the body by stimuli that, subsequently, must be compared with the actual consequences. When predicted and actual consequences match the process ends; when there is a mismatch, a prediction error is computed, and the priors should be updated to explain away the errors and reduce surprise. Importantly, predictions do not have the same relevance since ambiguous signals require greater efforts and an inferential process to minimize the prediction error. The main effect of spatial perspective, regardless of identity, is not trivial but, rather, consistent with bodily illusion literature. Indeed, these experimental manipulations show that external objects as, for instance, rubber hands (Botvinick & Cohen, 1998; Costantini & Haggard, 2007b; Kalckert & Ehrsson, 2014) or virtual bodies (Maselli & Slater, 2013; Pyasik et al., 2022), can be misattributed to the self if stimuli are presented in a first-person perspective but this happens regardless its visual appearance (i.e., identity). In other words, predictions rooted in perspective, being highly unambiguous (i.e., it is highly likely that the self-hand appears in the first-person perspective), overwhelm those created from identity (i.e., visual features can vary along a wide range of states). This mechanism is highly adaptive

being able to overcome the frequent changes of perceptual features of the own hand (e.g., wearing gloves), whereas the point of view is fixed across the experience. In other words, perspective cues are sufficient in several daily-life situations. As for the conscious priming, it is worth of noticing that a prime provides per se additional cues that can potentially act upon the ongoing unconscious processes in a top-down fashion. Not surprisingly, here priming affected the unconscious response only within the first-person perspective, namely the level of the only variable displaying an unconscious advantage. However, self-face priming provided unambiguous information (i.e., self-face) so that these cues are irrelevant because redundant, and perspective remain sufficient to unconsciously attribute the hand to the self (even if it belonged to another person). The prime exerted an effect only in the most 'critical' condition, namely with other-hands stimuli, and not with self-hand stimuli. In other words, when both the conscious prime and stimulus belonged to another person were administered, the first-person advantage was lost because of the presence of the highest degree of ambiguity. In short, priming resulted effective only when the probability of that stimulus to be unequivocally coded as self-related was the lowest. This, in turn, slowed down the conscious access possibly because of a prediction update process. Interestingly, this is in line with the idea that the content of visual awareness emerges once prediction errors are minimized through the prediction and sensory evidence verification cycle, and with the fact that, under conditions of stimulus ambiguity, not only prior beliefs act upon stimulus prioritization, but also prioritization can be extended to other-related stimuli (Falbén et al., 2020).

Summarizing, our results suggest that self-attribution of bodily stimuli before visual awareness relies on spatial perspective except for very ambiguous circumstances that necessitate higher order resources. These findings extend the link between ownership attribution, self-relevance prioritization effects, and the predictive processing hypothesis, highlighting the importance of top-down feedback projections for the content of conscious perception (Hohwy & Seth, 2020; Lamme & Roelfsema, 2000). Additionally, our findings suggest that the visual system in general gives precedence to corporeal stimuli belonging to the self as compared to another person. Interestingly, this is consistent

with the Self-Attention Network (Sui & Humphreys, 2015) showing that self-related information enjoy enhanced perceptual processing as a consequence of bottom-up attentional capture or higher order mechanisms such as, for instance, decision making or memory, here capitalized by spatial perspective but not identity.

Before concluding, some limitations of the study should be emphasized. First, we tried to control for the well-known role of low-level features on unconscious processing by creating stimuli under rigorous experimental constraints. Most importantly, stimuli were the same in the two perspectives and self-hand stimuli were used as other-hand stimuli for the subsequent participant (i.e., we alternated the same stimuli, keeping the same low-level features and only changing their high-level meaning in the eye of the observers). One might still argue that the different (i.e., mirror) shade due to a 180° rotation could have had a role. Despite we cannot exclude such option, it fails to explain the interaction we reported here. Second, self-stimuli constitute the most familiar perceptual objects of our existence, thus making hard per se to control for visual familiarity that might influence the results. Here we adopted experimental rather than personal familiarity, thus whereas we can conclude that this effect is not driven by the mere visual familiarity, how personal familiarity could act on the investigated mechanism is worth investigating. Moreover, the interaction we report is certainly driven also by other-related features (i.e., other face and hand). Third, it is worth noticing that the priming task we adopted here differs from classical approaches being primes consciously perceived and objects of a memory task in prime-check trials, unlike usual priming tasks in which primes are even unaware or ignored. We adopted such solution to investigate conscious priming effects on visual conscious access, as in Stein and colleagues' work (Stein et al., 2023). As the conscious access indexed by the bCFS paradigm is particularly sensitive to the working memory content (Pan et al., 2014), we've added such task to maximize top-down prime effects on visual processing. It cannot be excluded that such approach was crucial for our findings, or whether the same results could have been obtained with more classical approaches. A fourth limit regards the absence of an object condition as a prime or, more importantly, as a target. Consequently, our study focusing on bodily attribution

cannot generalize its findings to the general category of self-associated stimuli, an interesting topic worth of future investigations. Similarly, being bCFS rooted on a conscious measure of subjective visibility, it cannot exclude response biases (Stein, 2019) and, consequently, more stringent techniques relying on objective awareness measures (Stein & Peelen, 2021), could be employed to expand our findings to objective unconscious perception.

2.3.5 *Interim Conclusions*

Summarizing, results from *Study* 1 (Ciorli & Pia, 2023) and *Study* 2 (Ciorli & Pia, 2024) suggest that self-attribution of bodily stimuli before visual awareness mostly relies on spatial perspective, except for very ambiguous circumstances that necessitate higher-order resources. These findings support the fact that self-other distinction is a crucial mechanism for maintaining a pre-reflective form of BSC that is built before awareness and prioritized into consciousness, as our body is the most relevant object of the environment. Such mechanisms seem to be mostly driven by predictions on bodily perspectives associated with the self.

Considering such results, in the next study we investigated whether this pre-reflective form of self-other distinction might nevertheless produce ownership over the hand stimulus at an unconscious level.

2.4 Study 3: **Visual Awareness is not required for the Virtual Hand Illusion: a combined protocol of Virtual Reality and Continuous Flash Suppression**

Ongoing

Ciorli, Pyasik, Trombetti, Costanzo, Kalckert & Pia

2.4.1 *Introduction*

As previously mentioned, self-other distinction and self-recognition are two interrelated key mechanisms aimed at distinguishing between our physical body and the external world. This physical boundary creates a sense of the bodily self that is separate from other objects. The subjective feeling that this physical body is imperishably my own body as long as I exist is termed body ownership (BO), which is defined as the sense that one's body belongs intrinsically to oneself and it is always present in one's own mental life (Gallagher, 2000; James, 1890; Merleau-Ponty & Smith, 2006; Tsakiris, 2010). BO is thought to emerge from the integration of multiple sensory inputs, such as visual, tactile, and proprioceptive signals, that create a coherent and unified experience of the body (Driver & Noesselt, 2008; Tsakiris, 2017). Historically, the fact that one's own body is a permanent presence in experience made the study of BO particularly challenging, given that in neuroscience it's crucial to compare the presence with the absence of a certain phenomenon. However, the scientific study of BO has been made possible through bodily illusion paradigms, such as the Rubber Hand Illusion (RHI; Botvinick & Cohen, 1998) or the Full-Body Illusion (Maselli & Slater, 2013; Petkova & Ehrsson, 2008; Pyasik et al., 2022; Slater et al., 2010).

In the RHI, a fake human-like hand is placed in a bodily-congruent position, whereas the real hand of the participants is sight-occluded and placed external to the body midline. By synchronously

stroking the fake and the real hand with participants looking at the fake hand, after a few seconds (the onset of the illusion is generally around 15 seconds; Finotti et al., 2023; Lloyd, 2007) the participant reports the feeling that the fake hand 'is like their hand', with the feeling of an ownership experience, despite the clear cognitive belief that it's a fake hand. In other words, the rubber hand is integrated into the body schema subserving BO, a mechanism called embodiment. The effectiveness of the illusion is measured by both explicit and implicit measures such as, respectively, ownership questionnaires (exploring the subjective and phenomenological experience of BO) and proprioceptive drift, which refers to the shift or change in the perceived position of one's body part, typically towards the location of the fake hand when embodiment occurred. Proprioceptive drift is an example of how the brain integrates and resolves competing sensory information from different modalities - like vision, touch, and proprioception (the sense of the position of body parts) - to form a coherent experience of body ownership. The predictive coding theory applied to BSC highlights that embodiment emerges as a consequence of resolving the multisensory conflict between the visuo-tactile stimulation over the fake hand and somatosensory/top-down information of the real unseen hand (Apps & Tsakiris, 2014). Such conflict arises when predictions, based on internal models explaining sensory events (i.e., multisensory integration is experienced in my body), do not meet the sensory feedback, generating a prediction error, that in the RHI is resolved in favor of visual inputs associated to tactile sensations, consequently attenuating somatosensory ones and integrating the fake hand in one's body schema (Limanowski & Blankenburg, 2015; Zeller et al., 2016).

A tidal wave of studies in the last quarter of the century took advantage of the RHI paradigm to explore the mechanisms that generate embodiment and the feeling of ownership. In a review, Blanke, Serino e Slater condensed the principles subserving BSC and the necessary constraints for experiencing BO (Blanke et al., 2015). Four determinants of BO have been highlighted: the proprioceptive (or postural) constrain, for which a fake hand must be placed in a bodily-congruent position (i.e., first-person perspective), whereas incongruent bodily positions do not lead to

ownership; the body-related visual information (or anatomical) constrain, for which the object must have a human-like shape; the peripersonal space constraint, implying that the fake hand must be placed also within the peripersonal space of the subject; finally, the embodiment (or multisensory integration) constraint, for which there must be congruency of multisensory stimulation (usually visuotactile or visuomotor) between the real and the fake hand. If such BSC 'rules' are applied, body ownership can be induced, manipulated and measured. However, it must be noted that around 70% of the population are subjected to the illusion, whereas the others seem not to be affected by (the so-called 'non-responders'; Ehrsson et al., 2004b; Kalckert & Ehrsson, 2014; Riemer et al., 2019). In recent years, the RHI has been extended also to virtual reality, allowing to experience ownership over a virtual hand or even an entire virtual body as in the Full-Body Illusion (Maselli & Slater, 2013; Pyasik et al., 2022).

Despite the large body of studies investigating BO, there is a gap in the literature on the relation between BO and awareness (Faivre et al., 2015b). Looking at BO determinants, *Studies* 1 and 2 of the present work confirmed that a) spatial perspective (postural constraint) can be processed before awareness, with a prioritization of the 1PP (Ciorli & Pia, 2023, 2024); b) that hands identity does not affect visual awareness, as well as it does not affect embodiment (anatomical constraint). Thus, is it possible that BO might arise before conscious perception, if also the peripersonal and multisensory integration constraints are respected? Is BO built as an automatic mechanism to have a primitive form of bodily-self (un)consciousness? Are unconscious multisensory processes sufficient to induce a change in BSC? We investigated these questions in this study, in which we combined Virtual Reality and the CFS paradigm (see Chapter I, section 1.3). Specifically, we applied the Virtual Hand Illusion (VHI; Sanchez-Vives et al., 2010) paradigm, which is a virtual version of the RHI, while in the dominant eye of the participants a Mondrian pattern was projected to mask from awareness the vision of the hand, while keeping the tactile stimulation above the sensory threshold. Crucially, a few studies suggest that multisensory integration can occur even if one modality is

unconsciously perceived (Deroy et al., 2014, 2016; Mudrik et al., 2014; Zher-Wen & Yu, 2023b). Precisely, the congruency between a consciously perceived stimulus within a modality (usually visual) and an unconsciously perceived stimulus within a different sensory modality (i.e., auditory; Alsius & Munhall, 2013; Chen et al., 2011; Chen & Spence, 2010; Lupyan & Ward, 2013; Ngo & Spence, 2010; Palmer & Ramsey, 2012; tactile; Hense et al., 2019; Lunghi et al., 2010, 2017; Salomon et al., 2016, 2017; Van Der Hoort et al., 2017; olfactory; Zhou et al., 2010; proprioceptive, Salomon et al., 2013; vestibular; Salomon et al., 2015), leads to an enhancement in the experimental performance, or a drop following incongruent stimulation (for a review, see Mudrik et al., 2014). These processes are likely to depend on long-range connections across sensory cortices, as well as on possible multisensory integration sites such as the posterior parietal cortex, the superior temporal sulcus (Driver & Noesselt, 2008), or more anterior cortices (Dehaene, 2001b; Dehaene & Changeux, 2011)**.** So far, only two studies investigated the role of BO in visual awareness: Van der Hoort and Ehrsson (2017) showed that BO can enhance perceptual dominance of the embodied hand in a BR task, suggesting a link between BO and visual awareness (Van Der Hoort et al., 2017), whereas Solomon and Colleagues (2017) highlighted that multisensory integration of visuo-tactile bodily signals can occur without conscious perception and can consequently shape the bodily boundaries (i.e., the peripersonal space; Salomon et al., 2017). However, no study yet investigated whereas and how BO can emerge unconsciously. In this study we manipulated Spatial Perspective (first vs third-person perspective; 1/3PP), congruency of the visuotactile stimulation (synchronous/asynchronous; Synch/Asynch) and awareness of the virtual hand (aware/unaware) through CFS to test this hypothesis. We hypothesized that BO, as measured by the proprioceptive drift (the extent to which the real hand is mislocalized towards the fake hand), would still occur in absence of visual awareness.

2.4.2 *Methods*

Participants

Thirty-six subjects (20 F, mean age = 26.9 ± 4.7 years) with normal or corrected-to-normal vision participated in the study. In the first screening procedure (see the next section), participants were selected based on the following criteria: 1) the presence of the illusion at the conscious level (N = 21); onset of the illusion not greater than 20 seconds (N = 15), as a greater time would render the suppression of the virtual environment extremely hard to achieve. The 15 participants satisfying the inclusion criteria participated in the main experiment. Of those, participants in which the virtual hand broke the mask suppression in the unconscious trials for more than 5 seconds (N = 6) were excluded (see the statistical analysis section). Thus, the final sample size resulted in N = 9. They were all naïve to the research question of the study, which was approved by the Ethical Committee of the University of Turin (protocol n. 0486683) and performed under relevant guidelines of the declaration of Helsinki.

Setup and procedure

The experiment was conducted in a single session that lasted approximately 2 hours. Firstly, participants were administered a binocular rivalry task to test their eye dominance (Acquafredda et al., 2023). This was followed by the first screening for the susceptibility to the VHI where the complete VHI procedure and questionnaires and proprioceptive drift measurements were performed; for the selected participants, it was followed by the second screening to determine the individual VHI onset time. Finally, the main experiment was administered with 6 VHI conditions (3 conscious, 3 unconscious VHI); all procedures are described in detail below.

Eye dominance

Eye dominance was measured in order to detect the dominant eye with a bCFS (see method section) task. A target hand was shown to one eye, while a dynamic Mondrian pattern, updating at a frequency of 10Hz, was shown in the other. The Mondrian's contrast, initially at 100%, gradually ramped down to 0% between the first second of trial onset to 8 seconds. By contrast, the target started

at 0% of contrast and gradually ramped up to 100% within the first second of the trial. Participants had to respond as soon as possible once the target broke the suppression with respect to the given location (up-top arrow; down-bot arrow). The block was made by 36 trials, in cui 18 times the target was shown to the left eye, and 18 in the right eye, counterbalancing stimulus location. At the end of the block, mean reaction times for each eye were computed, and the eye with faster reaction times (i.e., faster conscious access) was considered the dominant eye.

Virtual hand illusion

Stimuli and setup

The VHI scenario was developed and implemented in Unity 2017 game software environment (http://unity.com) and presented via Meta Quest 2 head-mounted display (HMD; https://www.meta.com) with 6 degrees of freedom, a 113.46° field-of-view (diagonal FOV) and a resolution of 1832 x 1920 per eye.

The virtual scene contained a dark room with a table (90 × 60 cm, scale 1:1) and an avatar (scale 1:1, light-skinned) positioned in front of the table with its right hand and wrist placed on the table, palm down. A virtual black cloth covered the space between the avatar's right hand and its neck, thus covering the avatar's upper body and the space between the table and the avatar's torso. This was done in order to present only the virtual hand, rather than the entire virtual body, thus mimicking the RHI setup (Botvinick & Cohen, 1998). In addition, a red circle (diameter 5 cm) was placed under the palm of the avatar's right hand to mark its location which was later used as the gaze fixation point (see details below).

During the VHI induction phase, synchronous visuo-tactile stimulation was administered by presenting flashes of purple light (RGB: 101, 11, 148; diameter of flash: 5 cm) to the dorsum of the virtual hand, which was combined with vibrotactile stimulation administered to the corresponding location on the participant's hand dorsum. The vibrotactile stimulation was delivered via a mini

vibration motor (diameter x height = 10 mm × 3 mm, 3 V, Rated speed – 12,000 RPM) controlled by an Arduino microcontroller (https://www.arduino.cc) with a custom-made script. The frequency and duration of each flash/vibration pulse were 0.27 Hz and 500ms, respectively.

In the unconscious VHI conditions, a dynamic high-contrast Mondrian-pattern mask flashing at 10Hz was presented to the participant's dominant eye during the stimulation phase, occluding the entire virtual scene, while the VHI scenario was presented to the non-dominant one. In the conscious VHI conditions, the scenario was presented to both eyes.

Procedure

Screening 1. The complete VHI procedure was administered to evaluate participants' susceptibility to the VHI in terms of subjective embodiment and behavioral shift of the perceived self-location of the hand (proprioceptive drift). To be eligible for the study, participants had to demonstrate both indices of embodiment because 1) the presence of subjective embodiment was required to estimate the illusion onset that would also be used in the main experiment; and 2) the proprioceptive drift was the key experimental measure in the main experiment, since subjective embodiment cannot be achieved in unconscious VHI conditions. The VHI followed the standard RHI-like protocol that included pre-stimulation proprioceptive judgments, stimulation phase, post-stimulation proprioceptive judgments, and embodiment questionnaire.

At the beginning of the experiment, participants, wearing the HMD, were seated in front of the table and their right hand was placed in front of them, palm down, 30 cm to the right of their body midline; the vibration motor was attached to their hand dorsum with medical tape. Participants were instructed to remain still throughout the experiment and to keep their right hand relaxed. From the moment when the participants put on the HMD, the virtual scene was occluded and only the black background was visible.

During the *pre-stimulation proprioceptive judgments* phase, participants saw a white horizontal line (220 cm long) with a green cursor (triangle) in front of them. They were instructed to position the cursor by moving it left and right with left and right arrow keys that they pressed with their left hand, in the location that corresponded to the location where they perceived their unseen right middle finger to be. Participants were additionally instructed that the length of the line had no reference to the real space or the real table. The proprioceptive judgments were collected for 6 trials. Once they were completed, the line and the cursor disappeared from the screen and the *stimulation phase* started. Firstly, participants saw only the virtual table and the red mark on the table; they were instructed to familiarize themselves with the environment and then to keep their gaze on the red mark. Then, the virtual hand appeared above the red mark on the table and was located 20 cm to the left of the participants' real right hand, i.e., 10 cm to the right of the body midline, and the visuo-tactile stimulation was delivered for 60 s. The stimulation was synchronous, i.e., the vibration pulses and the flashes were simultaneous. After the stimulation was completed, the virtual scene was occluded and the *post-stimulation proprioceptive judgments* were collected for 6 trials following the procedure identical to the pre-stimulation ones. Finally, the embodiment questionnaire was administered. Each questionnaire statement was presented separately on a black background, with a visual analog scale (VAS) below the statement. A cursor was placed in the middle of the scale and the left and right extremes were marked with "-" and "+", respectively. Participants were instructed that the statements referred to the virtual scene that they had just seen, and they were asked to express their level of agreement/disagreement with each statement by positioning the cursor on the VAS where the left pole ("-") represented complete disagreement, the right pole ("+") complete agreement and the middle of the VAS corresponded to uncertainty. The questionnaire consisted of 9 statements, as in (Pyasik et al., 2020), with 3 statements describing the feeling of ownership of the virtual hand, 3 statements referring to the feeling of disownership of the corresponding fake hand, and 3 control statements to control for participants' compliance and understanding of the task. The statements were presented in randomized order and the responses registered on the VAS were extracted as values from 0 to 100.

The individual susceptibility to the VHI was established based on the proprioceptive drift values and the questionnaire ratings. In particular, to obtain the value of the proprioceptive judgments, the difference between the perceived and the actual location of participants' right hand (in cm) was obtained for each trial. The proprioceptive drift was then computed as the difference between the post- and pre-proprioceptive judgments in each trial, averaged between trials. More positive values represented a greater proprioceptive shift towards the virtual hand. As regards the subjective embodiment, for screening purposes, we considered the ratings in the statements that directly concerned body ownership, rather than self-location, namely "*I felt as if I was looking at my own hand*" and "*I felt as if the Virtual Hand/Virtual Object was part of my body*". The cutoff for illusion susceptibility was set at the proprioceptive drift of at least 2 cm [based on the previous VHI study (Pyasik et al., 2020) and the average values of proprioceptive drift reported in the experimental conditions of the RHI studies] and the ratings of at least 55, i.e., over the midpoint of the VAS, in the two embodiment questions.

Screening 2. Participants susceptible to the VHI in Screening 1 proceeded with the next part of the study aimed at determining their subjective onset of the VHI and whether the illusion susceptibility remained stable if the stimulation duration was reduced to the duration equal to the onset. To this end, firstly, participants were presented only with the stimulation phase, identical to that described above, and were instructed to indicate verbally the first moment in which the virtual hand began feeling like their own. This procedure was repeated three times. The average of the response times (in seconds) was considered as the VHI onset. This procedure was made to assess and use the minimum subjective time for the occurrence of the VHI since the exposure time is critical for the CFS procedure. Indeed, the longer the trial, the greater the possibility of breaking the suppression induced by a 2-D Mondrian mask over a 3-D virtual scenario, as masks are more effective the greater the similarity with the masked target (Breitmeyer & Öğmen, 2007). Therefore, for the unconscious VHI conditions in the

main experiment, the cutoff for the onset time was set at 20s maximum, not including participants with a greater onset timing.

Then, the complete VHI procedure identical to Screening 1 was repeated with the stimulation duration that was set to the individual VHI onset time. The proprioceptive drift and the subjective embodiment were used as the selection criteria with the same cutoffs as in Screening 1. Selected participants proceeded with the main experiment.

Main experiment. In each condition, the experimental procedure followed the same steps of the VHI as in the two screenings. The stimulation duration was set to the individual VHI onset time from Screening 2, the proprioceptive judgments were registered in 3 trials pre- and post-stimulation, and the embodiment questionnaire was reduced to 2 statements that required a verbal yes/no response, as in (Chancel et al., 2022). One question probed the feeling of embodiment (in conscious VHI conditions: *"Did it feel as if the virtual hand was your hand?"*; in unconscious VHI conditions: *"If you had to guess, do you think that you were exposed to the condition that would lead to you feeling as if the virtual hand became your hand?"*), and the other question assessed the number of times that the stimulus (virtual hand) broke through the mask in the unconscious VHI conditions (*"Did you see the virtual hand? If yes, could you estimate for how many seconds?"*). The second question was included also in the conscious VHI conditions in order to keep the procedure identical and to control the participants' compliance.

The conditions differed in three aspects: type of stimulation (synchronous/asynchronous), perspective of the virtual hand (first-/third-person perspective, 1PP/3PP) and virtual scene visibility (conscious/unconscious), but without mixing the double control conditions represented by asynchronous stimulation + 3PP perspective, neither in the conscious nor in the unconscious condition (see **Fig. 2.5**). In the three *conscious VHI conditions*, i.e., where participants saw the virtual scene, the main experimental condition was the one where the virtual hand was presented in the 1PP and stimulated synchronously, as in the screenings. The two control conditions were introduced to

differential control for the effects of stimulation and perspective. They were, respectively, the 1PP condition with asynchronous stimulation, where the flashes and the vibration pulses were delivered in the opposite phases rather than simultaneously, and the 3PP condition, where the stimulation was synchronous, but the view of the virtual hand was rotated 180° as if participants were seating across from it. Both those conditions are known to not induce embodiment in the RHI and VHI (e.g., Burin et al., 2017; Pyasik et al., 2020; Tsakiris, 2010) and could shed light on the contributions of the different cues of embodiment in the unconscious VHI conditions. The *unconscious VHI conditions* were identical to the conscious ones with the addition of the high-contrast mask that was presented to the dominant eye throughout the stimulation phase. The mask was positioned in a way that led it to occlude the entire virtual scene.

Each condition consisted of multiple trials (as in Chancel et al., 2022) where one trial is the complete VHI procedure with measurements (proprioceptive judgments and questionnaire), as described above. The conscious VHI conditions included 3 trials each. In the unconscious VHI conditions, the aim was to obtain 3 trials in which the virtual hand did not break the suppression induced by the mask, i.e., had not ever been seen. Therefore, if participants replied "yes" to the question about seeing the virtual hand, the trial was discarded and another trial was administered; a maximum of 6 trials was administered per condition. In case an unconscious VHI condition was completed (6 trials) but less than 3 trials without the virtual hand breakthrough were obtained, the trials with the shortest perceived visibility were selected. The effects of the hand visibility on embodiment during the unconscious VHI conditions were controlled at the end of the experiment by administering one trial of the main embodiment condition (conscious, 1PP, synchronous stimulation) with the duration of stimulation set to the longest perceived visibility across the selected trials of all unconscious VHI conditions. If the duration of the stimulation equal to the longest stimulus breakthrough time did not evoke embodiment in the main embodiment condition, it would be possible to assume that it did not affect the levels of embodiment in the unconscious VHI.

The order of conditions was randomized according to the Latin square. For each condition, proprioceptive drift was computed as in the screenings and averaged between trials. The proportion of responses "yes" to question 1 (embodiment) was considered as an index of subjective embodiment.

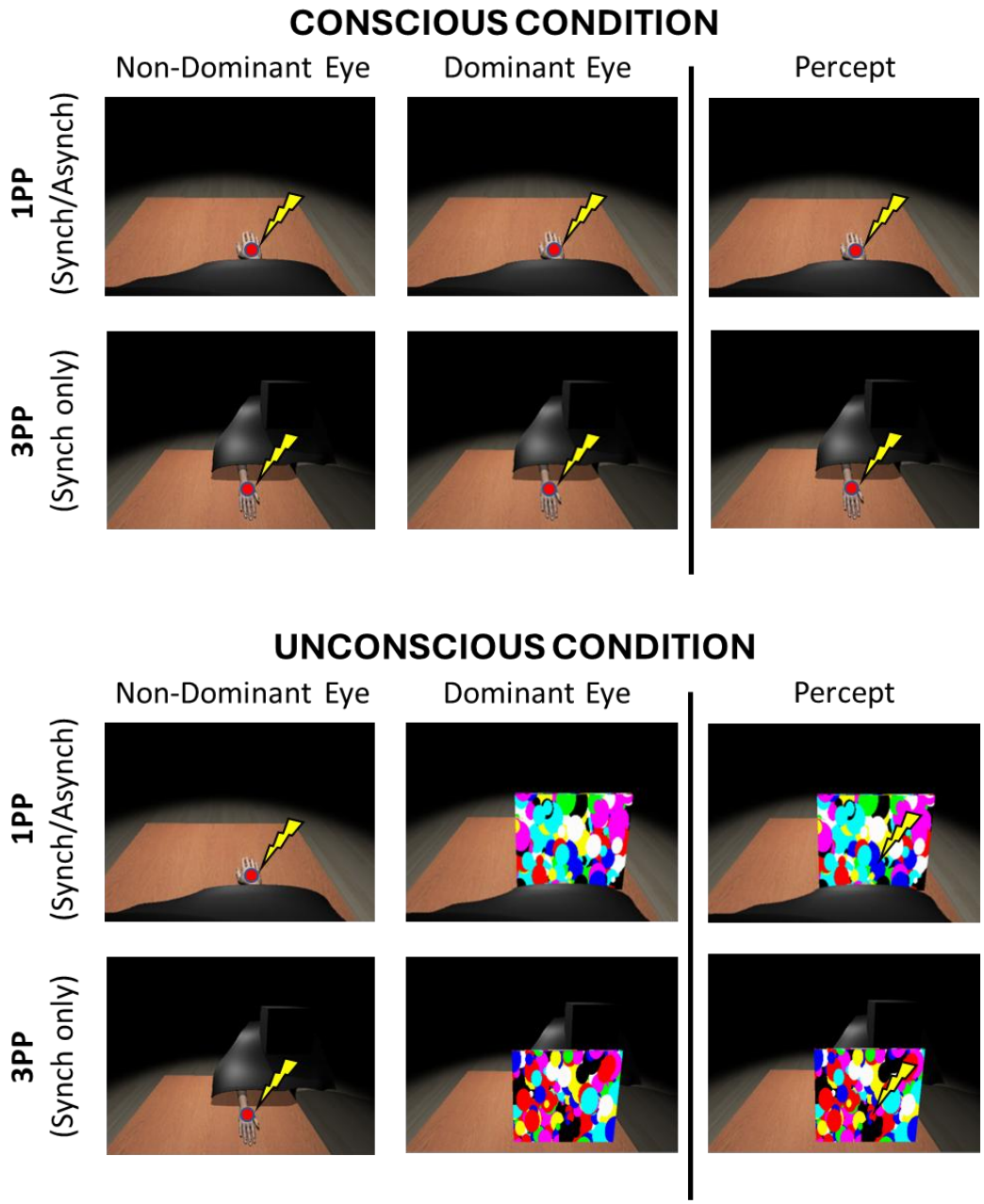

***Figure 2.5**: Schematic representation of the Virtual environment for the VHI task, within the conscious and unconscious conditions, in First and Third-person perspectives. Tactile sensory stimulation was always above sensory threshold. Vision of the hand was masked in the unconscious condition, for which wither the spatial perspective or the synchrony of the visuo-tactile stimulation was not consciously perceived.*

Statistical analysis

Participants reporting unstable binocular perception (N = 0), those for which the virtual scenario broke the suppression for more than 5s (N = 5) were excluded from the analysis. Data were normally distributed (Shapiro Wilks < .05) with the exception of the Unconscious-3PP-Synch condition, and non-parametric analysis was performed when involving such condition. We then conducted a one-way rm ANOVA on the mean post-pre proprioceptive drift for the conscious conditions to test the efficacy of the classic VHI procedure with the factors 1PP-Synch, 1PP-Asynch, and 3PP-Synch. Then, we conducted another one-way non-parametric rm ANOVA within the same but unconscious conditions to test for the presence of the embodiment at the unconscious level. Finally, we performed a 2x2 rm ANOVA with the factors *Awareness* (Conscious, Unconscious) and *Stimulation* (Synch, Asynch) to compare the proprioceptive drifts within the 1PP.

2.4.3 *Results*

Conscious conditions

The one-way rm ANOVA on the mean post-pre proprioceptive drift for the *conscious* conditions with the factors 1PP-Synch, 1PP-Asynch, 3PP-Synch revealed a significant effect of the condition ($F_{(2,16)} = 6.67$, $p < .01$, $\eta_p^2 = .488$), and post-hoc comparisons showed that the condition 1PP-Synch yielded a significantly greater proprioceptive drift as compared to the 1PP-Asynch ($t_{(8)} = 3.38$, $p < .05$, Cohen's $d = 1.19$) and 3PP-Synch ($t_{(8)} = 2.43$, $p < .05$, Cohen's $d = 0.86$) conditions, suggesting that the embodiment was present only in the experimental but not in the control conditions (see **Fig. 8**).

Unconscious conditions

The one-way non-parametric rm ANOVA on the same factors (1PP-Synch, 1PP-Asynch, 3PP-Synch) during *unconscious* trials showed a significant effect of the condition on the proprioceptive

drift ($\chi^2_{(2)}$ = 6.89, p < .05, Kendall's W = .38). Post-hoc analyses with Wilcoxon signed-rank tests revealed that the proprioceptive drift in the 3PP-Synch was significantly lower from the drift in the 1PP-Synch (W = 33, Z = 2.1, p < .05, r = .83) and the drift in the 1PP-Asynch condition (W = 31, Z = 1.8, p < .05, r = .72), suggesting that embodiment occurred only in the 1PP but not in the 3PP condition irrespectively of the Stimulation (see **Fig 2.6**).

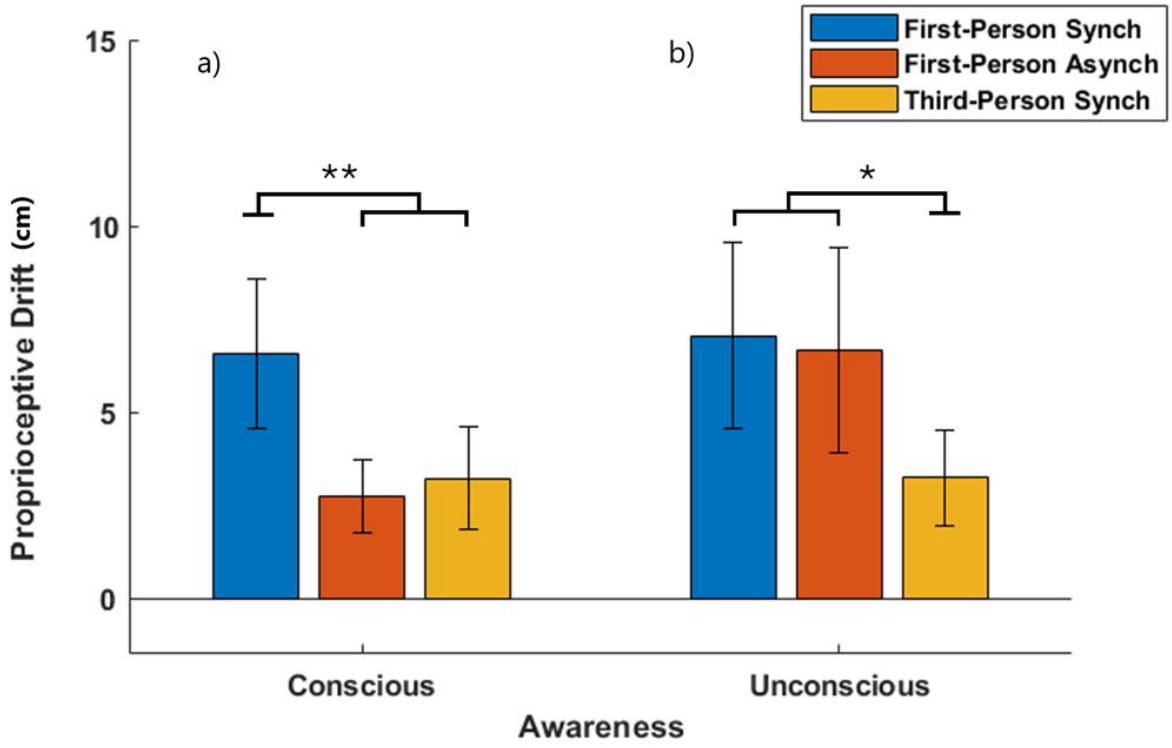

Figure 2.6*: a) shows the results from the conscious condition, showing greater Proprioceptive Drift in the First-Person synchronous condition only (cm ± SD). b) shows the results from the unconscious condition, showing greater Drift in both the synchronous and asynchronous First-, but not the Third-, Person perspective conditions (cm ± SD). *p < .05, **p < .01, ***p < .001*

Control Analysis

Of the included participants, only 5 of them completely suppressed the virtual hand, whereas the other 4 consciously perceived in a few trials (~38% of unconscious trials) the hand for a mean time of 2.8 ± 1.3s. Thus, it is possible that the proprioceptive drift effects we observed in the unconscious condition could have been driven by such conscious perception timing. To rule out this hypothesis, participants performed a conscious 1PP-Synch condition for a timing corresponding to the longest timing of conscious perception of the hand in the unconscious trials (max 4s) in order to test whereas such timing was sufficient to produce the observed drift. Such proprioceptive drift measure was confronted with the drift obtained in the unconscious 1PP-Synch condition. T-tests showed that the control drift was significantly lower as compared to it ($t_{(3)} = 3.57$, $p < .05$, Cohen's $d = 1.78$), which indeed was not significantly different from 0 as showed by a one-sample t-test ($p = .52$). This suggests that short conscious exposure to the virtual hand is not sufficient to produce the observed drift in the unconscious 1PP-Synch condition, suggesting a crucial role of unconscious exposure timing.

2.4.4 *Discussion*

In this study we tested whereas BO over a virtual hand could emerge without visual awareness through the combination of Virtual Reality and CFS; specifically, we manipulated Spatial Perspective (1/3PP), the congruency of the visuo-tactile stimulation (synchronous/asynchronous) and awareness of the virtual hand (conscious/unconscious) to explore the role of visual awareness on the proprioceptive drift in a VHI experiment. Results showed that, at the conscious level, embodiment was induced only in the classical experimental condition respecting the constraints for embodiment (i.e., in the 1PP-Synch condition). Crucially, the same phenomenon occurred also when the virtual environment was perceived unconsciously – however, the congruency of the stimulation did not affect the proprioceptive drift, which was induced by the mere presence of a 1PP virtual hand despite the stimulation's congruency. A hand violating the postural constraint (i.e., 3PP), consciously or unconsciously perceived, did not trigger the drift. This data, which is important to outline that are

preliminary given the small sample size, suggests that visual awareness is not required for embodiment, and that objective ownership responses might be modulated by unconscious processing of bodily perspective.

The finding for which bodily perspective can modulate bodily self-attribution per se is in line with several other evidence, both at the conscious (Apps & Tsakiris, 2014; Blanke et al., 2015; Brady et al., 2011; Tsakiris, 2010, 2017) and unconscious levels (Ciorli & Pia, 2023, 2024). In the previous studies of this thesis, we showed that the first-person hand perspective enjoys privileged access to consciousness and that predictions rooted in perspective have a crucial weight for self-attribution despite the hand's appearance and top-down identity contexts, being almost inevitably attributed to the self unless for ambiguous circumstances (Ciorli & Pia, 2023, 2024). Our data shows that, within the constraint of the peripersonal space, 1PP can elicit embodiment automatically, even when we lack visual awareness of the body part. Crucially, the synchrony of visuo-tactile multisensory stimulation was not found to affect this phenomenon, as 1PP embodiment occurred similarly in both synchronous and asynchronous conditions. Specifically, synchronous tactile stimulation influenced conscious but not unconscious 1PP embodiment. Though counterintuitive, such a finding aligns with full-body illusion studies showing that 1PP alone can elicit subjective embodiment and proprioceptive shifts toward the virtual body, at least at the conscious level (for a review, see Pyasik et al., 2022). Neuropsychological evidence further supports such a view: for example, damaged brain-damaged patients with pathological embodiment (Garbarini et al., 2020) show that merely viewing a hand in a congruent bodily-self position can induce embodiment without multisensory stimulation. Similar findings have been observed in studies with tetraplegic patients (Scandola et al., 2014). This evidence suggests that 1PP alone may be sufficient to elicit embodiment and, whereas synchronous stimulation may enhance its strength, asynchronous stimulation might disrupt it by violating the predictions rooted on the bodily self, i.e., I experience sensory congruency only within my body. In *Study 2* we found that the advantage of the 1PP diminished only under conditions of maximal ambiguity, which delayed conscious access to 1PP hand stimuli (Ciorli & Pia, 2024). Synchronous multisensory

stimulation may influence BO only at the conscious level as a proxy for resolving ambiguities that conflicts with predictions about the bodily self, which is always experienced from a 1PP unified, synchronous, multisensory experience. The idea that asynchronous stimulation does not completely prevent embodiment, as suggested by our results, but rather weakens it is also supported by recent studies (Keenaghan et al., 2020). However, from our data, we can only speculate that vision alone may induce unconscious embodiment in 1PP, as our conditions always included synchronous or asynchronous tactile stimulation. Indeed, the effect we found may require additional sensory stimulation beyond the 1PP visual input, though this seems less likely, as other studies suggest that 1PP itself may be sufficient for embodiment (Keenaghan et al., 2020).

At the neural level, hand ownership is thought to emerge through multisensory integration in the intraparietal sulcus (IPS) and premotor cortex (Ehrsson et al., 2004b; Ehrsson, 2012; Gentile et al., 2013). The lateral occipital complex (LOC), particularly the extrastriate body area (EBA), processes hand images and differentiates between one's hand and others' (Downing et al., 2001; Myers & Sowden, 2008; Peelen & Downing, 2007). During hand ownership illusions, connectivity between the IPS and EBA increases, suggesting enhanced neural communication (Gentile et al., 2013; Guterstam et al., 2013; Limanowski et al., 2014) that may prolong visual dominance of the hand image (Van Der Hoort et al., 2017). Additionally, BO illusions activate frontoparietal areas associated with consciousness (Ehrsson et al., 2004b; Limanowski & Blankenburg, 2016b, 2016b), potentially affecting awareness of body image (Van Der Hoort et al., 2017). Notably, visual inputs, even when subliminal, may activate and influence PPS neurons (Salomon et al., 2017) within the posterior parietal and premotor cortices (Astafiev et al., 2004; Limanowski & Blankenburg, 2016a). Thus, it is possible that the parietal lobe, which is shown to be less affected by awareness manipulations (Fang & He, 2005; Hesselmann, 2013; Ludwig et al., 2016; Ludwig & Hesselmann, 2015; Milner, 2012; Zhan et al., 2018) and represents nearby stimuli in body-centered coordinates (Colby & Goldberg, 1999), might guarantee a quick unconscious integration of visual corporeal inputs allowing the generation of stable visuospatial representation of the own body regardless of visual awareness, and

that would consequently trigger a pre-reflective ownership and integration of the body part in the body schema.

To summarize and conclude, these data suggest that BO can emerge implicitly and automatically through the unconscious perception of a 1PP hand within one's peripersonal space. This unconscious form of embodiment and BSC might represent a fundamental automatic body monitoring mechanism essential for environmental interaction that operates independently of the complexity of conscious processing. Notably, this type of embodiment appears not to require multisensory integration, challenging the current definition of BO, which is thought to arise from integration processes across sensory modalities. Instead, multisensory integration may play a higher-order role by resolving conflicts that challenge predictions about BSC, likely influencing BO in a conscious top-down manner. Nevertheless, multisensory integration may be crucial for the subjective experience of BO as a reflective and high-order form of BSC. These findings indicate that BO and BSC might emerge prior conscious perception, as our bodies are inherently relevant and predictable objects. However, it is essential to note that these data and interpretations are preliminary. Our rigorous inclusion criteria (selecting only participants susceptible to the illusion and those effectively suppressing from awareness the virtual environment) make it challenging to achieve a large sample size, even though preliminary effect sizes are substantial. Thus, conclusions should be carefully approached as speculative at this stage.

Chapter III

On Face Identity processing in the absence of Awareness

3.1 *Face familiarity*

One of the most relevant objects for human and non-human primates are faces, as they have an innate predisposition for face detection (Morton & Johnson, 1991). Except for some neuropsychological cases, face recognition is a skill that humans highly developed and masters. From faces we can extract a huge amount of different information, such as age, ethnicity, gender, but also emotions, intentions, memories, and so on – basically, very useful features that are essential for social interactions and cognition. Indeed, it is not surprising that human have a widely distributed neural system dedicated to face perception (Axelrod & Yovel, 2013; Haxby et al., 2000; Tsao et al., 2008). The most influential model of face recognition poses the existence of a core face system responsible for the processing of invariant aspects of face perception (i.e., structural face processing), localized in the Lateral Occipital Complex (i.e., Fusiform Face Area, Occipital Face Aarea, Superior Temporal Sulcus; FFA, OFA, STS), and an extended system, in which other cognitive networks dedicated to the processing of face-variant aspects (i.e., emotional or memory-related processing) are recruited to provide holistic face representation (Haxby et al., 2000; See **Fig 3.1** and **Fig. 3.2**). Such segregation is further supported by fMRI (Wang et al., 2016) and electrophysiological studies, that in particular showed how different Event-Related Potential components differentially react to certain face features, such as the N170, a lower-level face detection component subserving face encoding (i.e., discriminating faces vs object; Rossion & Jacques, 2011) or the N250, associating such features to

other information such as face identity (Alzueta et al., 2019; Bentin & Deouell, 2000; Eimer, 2000; Paller et al., 2003).

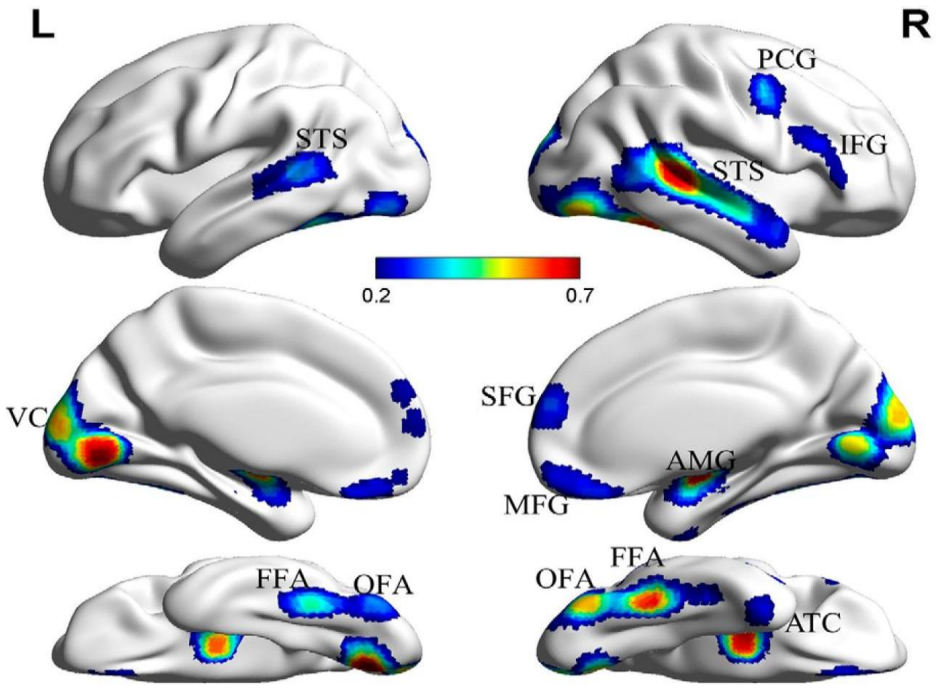

Figure 3.1*: This image is taken from Wang et al., 2016, showing face-selective probabilistic activation map. This study identified fourteen face-selective regions within old/new and face inversion tasks. Color bar represents the percentage of participants who showed face-selective activation. SFG, Superior frontal gyrus; MFG, medial frontal gyrus; PCG, right precentral gyrus; L, left; R, right.*

Perceiving a face, even if extremely natural and automatic, entails a cascade of brain processing that stems from the simple visual input to a multifaced representation, integrating visual, memory, emotional, empathy-related information. When we face a familiar person, we immediately recognize and activate such representation in order to have a proper social interaction. In fact, recognizing familiar faces is not just a mere visual task (Gobbini & Haxby, 2007). And neither it is recognizing one's own face, that triggers even more cognitive processes. In fact, our own face is inherently associated to self-consciousness and to other aspects that we don't experience in others, such as sensory processing, autobiographical memories, and temporal continuity of a first-person

living agent experience (Gillihan & Farah, 2005). The degree of familiarity of a given face seems to be a unique feature that creates a stimulus-processing advantage across a variety of tasks (Johnston & Edmonds, 2009). As previously mentioned in this dissertation, self-related stimuli entail behavioral advantages even over familiar stimuli, given their specialty for the brain. The self-face is indeed perceptually represented more robustly, as we experience it almost every day (Tong & Nakayama, 1999), it is associated with positive reward values (Ma & Han, 2010b), it attracts our attention (Devue & Brédart, 2008; Humphreys & Sui, 2016; Tacikowski & Nowicka, 2010), it is associated with our multisensory experience (Tsakiris, 2017). So, considering that also our face is a pivotal marker of our own identity, it is not surprising that self-stimuli enjoy enhanced processing within the brain, also in an automatic manner (Keenan et al., 1999, 2000). There is also evidence suggesting that the self-face is preferentially processed by the right hemisphere (for reviews, see Janowska et al., 2021; Molnar-Szakacs & Uddin, 2023), as suggested by behavioral (i.e., Keenan et al., 1999) and neuropsychological studies involving split-brain (Turk et al., 2002; Uddin, 2011; Uddin et al., 2005) and right-brain damaged (Breen et al., 2001; Gainotti, 2001; Yun et al., 2014) patients. Moreover, studies using various neuroimaging techniques (fMRI, EEG, PET, TMS) consistently highlighted a distinct pattern of right hemispheric brain activation during self-face recognition (Apps et al., 2012; Devue et al., 2007; Keenan et al., 2001; Morita et al., 2008; Sugiura et al., 2000; Taylor et al., 2009; Uddin et al., 2006), showing the activation of right inferior frontoparietal cortices and inferior occipitotemporal cortices (Hu et al., 2016; Morita et al., 2018; Platek et al., 2008; Sugiura et al., 2008) as key regions involved in self-face recognition.

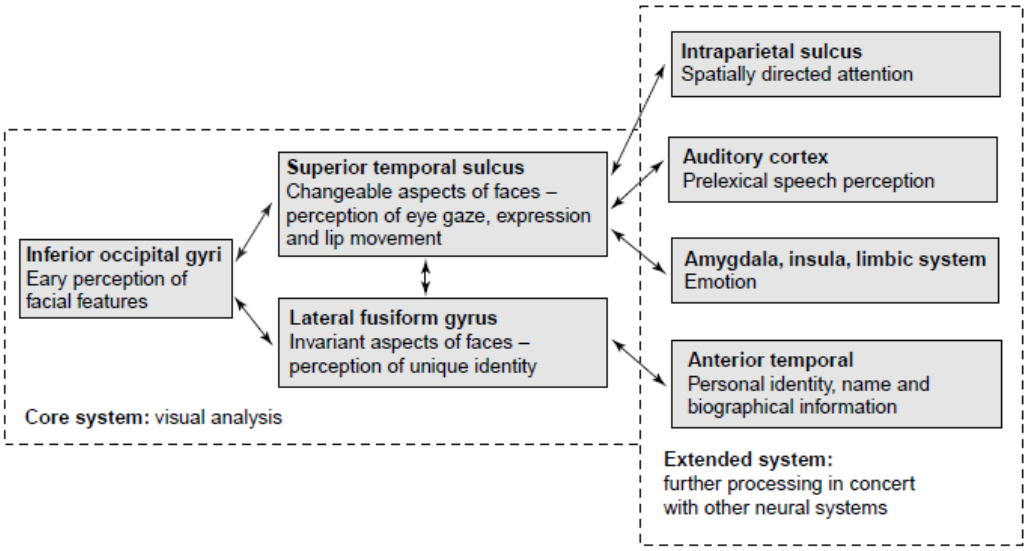

***Figure 3.2**: This image was taken from Haxby & Gobbini, 2000, representing the brain model subserving face processing. The core system deals with the encoding of the visual appearance of a face. The extended system extracts further information from faces and contributes in the retrieval of different aspects of person knowledge and emotional response.*

3.2 *Face Familiarity and Awareness*

Given the richness of information faces convey, it is not surprising that they are one of the most used visual stimuli in neuroscience, providing a unique opportunity to test how the different neural systems involved in face processing might relate to consciousness (Axelrod et al., 2015). Extensive research has shown that a lot of information conveyed by faces can be actually extracted without the necessity of conscious resources, as social cognition is extremely relevant and important for the human being (see **Fig. 3.3**). For example, facial configuration is processed before awareness, as shown by the well-documented face-inversion effect (Garrido et al., 2008; Lewis & Edmonds, 2005; Stein et al., 2016; Stein & Peelen, 2021; Van Belle et al., 2015; Zhou et al., 2010). Rotating a face upside-down disrupts configural or holistic face processing without altering low-level image information, and many studies showed that upright faces enjoy preferential processing at the unconscious level (Ciorli et al., 2024; Jiang et al., 2007; Stein et al., 2016; Stein, Hebart, et al., 2011; Zhou et al., 2010) that might rely on the activity of the FFA (Jiang & He, 2006; Kanwisher & Yovel,

2006; Yovel & Kanwisher, 2004). Such inversion effects do not occur for objects (i.e., Zhou et al., 2010). Besides basic configural processing, other social aspects conveyed by faces can be processed unconsciously, such as their emotional expressions (Gerbella et al., 2019; Hedger et al., 2015; Tamietto & de Gelder, 2010; Vetter et al., 2019; Williams et al., 2004; Yang et al., 2007) (but see: Gray et al., 2013; Qiu et al., 2022; Stein, Seymour, et al., 2014), gaze direction (Lanfranco et al., 2022; Stein, Senju, et al., 2011), personal traits (Freeman et al., 2014; Getov et al., 2015; Stewart et al., 2012), and also face familiarity, which not only relies on greater visual exposure experience during life, but entails also an affective component associated with. A couple of studies that used the bCFS paradigm observed that familiar faces enjoy faster access to consciousness compared to famous or stranger faces (Geng et al., 2012; Liu et al., 2022; Zhou et al., 2020). An EEG study found greater attentional capture induced by the self-face when unconsciously perceived as compared to faces for which participants acquired familiarity before the experiment (thus, without an affective component different from boredom; Bola et al., 2021), and a masking fMRI experiment showed differential subcortical responses between self and stranger faces, characterized by respectively the dopaminergic system and the amygdala activations (Ota & Nakano, 2021b). This body of work suggests that face familiarity represents an important social cue that might precede consciousness to be extracted.

Cognitive system	Cognitive subsystem	Type of face processing	Can it be processed unconsciously?
Social cognition	Emotions	Invisible facial emotions	Yes
	Social evaluation	Impression from a person based on invisible face (e.g., pleasantness, trustworthiness)	Yes
	Social cuing	Gaze and face view processing	Yes
	Familiarity and covert recognition	Familiarity processing of unconsciously presented faces (healthy participants) Covert face recognition in prosopagnosia	Yes Yes
Non-affective processing	Attention	Modulation of attention by invisible faces	mixed results, more studies are needed
	Multisensory integration	Integration of the invisible face and intact voice (variations of the McGurk illusion)	Yes
Face-specific processing	N/A[a]	Discriminating between face and non-face	Yes (dichotic paradigms) No (monocular paradigms)
	N/A	Discriminating between upright and inverted faces	Yes
	N/A	Processing unfamiliar face identity	No

[a]N/A, not applicable.

***Figure 3.3**: This table was taken from Axelrod et al., 2015. Such review resumes different aspects of face perception with related cognitive systems that are supported by unconscious processing.*

It is important to know that healthy participants do not represent the only way to study unconscious processing. Gold information about the brain functioning comes from Neuropsychology, the discipline aimed to study the damaged brain to understand the cognitive functioning of the intact brain. Given the unfortunately large sample of conditions and disorders of consciousness or conscious experiences, unconscious sensory processing has been extensively studied in neuropsychological research, particularly in patients with hemianopia and cortical blindness, also known as blindsight (Humphrey & Weiskrantz, 1967; Weiskrantz et al., 1974). These individuals suffer from damage to the primary visual cortex (V1), resulting in scotomas (i.e., blind portions of the visual fields) depending on the lesion size and site. Remarkably, some patients retain the ability to process stimuli presented within their blind field (for a review, see Cowey, 2010). These patients provide a unique model to investigate which stimulus features can be processed unconsciously in the absence of the primary visual pathway (the cortical genicular-striatal route), relying instead on the subcortical visual pathway: indeed, studies have demonstrated that features such as motion, shape, and emotional expression can be processed without awareness through the contribution of the subcortical structures activity (Ajina et al., 2020; Celeghin, De Gelder, et al., 2015; Tamietto & de Gelder, 2010). However, no studies to date have explored the processing of face familiarity in blindsight patients, leaving an intriguing gap in the understanding of unconscious face recognition mechanisms.

Another neuropsychological condition, rather than visual awareness per se, specifically targets face recognition, named Prosopagnosia (from the Greek, *prosōpōn* = face, *a-gnosis* = ignorance). Prosopagnosia is characterized by the selective impairments in recognizing and discriminating face identities, even close familiars, and sometimes even their own face (Casati et al., 2024). Such agnosia can be acquired after lesions within the ventral occipitotemporal cortex that are usually bilateral

(Benton, 1980; Damasio et al., 1982; Sergent & Signoret, 1992) in areas of the face network, such as FFA or the Inferior Occipital Gyrus (Gainotti & Marra, 2011; Rivolta et al., 2013). Interestingly, some individuals with prosopagnosia, despite being unable to consciously recognize faces, show distinct reactions to faces they have encountered before compared to novel ones, a phenomenon known as covert face recognition (Bruyer, 1991). Covert recognition manifests through indirect measures of face familiarity processing such as increased skin conductance responses (SCr), enhanced P3 event-related responses (for a review, see Rivolta et al., 2013), but also faster reaction times in indirect tasks (Bate et al., 2009; Bruyer, 1991; De Haan et al., 1991; De Haan et al., 1987; Rivolta et al., 2012). Thus, prosopagnosia and hemianopia cases provide outstanding opportunities to study face processing outside awareness.

Within the framework of this thesis, scientific literature already highlighted the fact that the self-face is differentially processed and prioritized before awareness, and that familiarity processing might occur without the direct involvement of conscious resources through unconscious or covert processing. However, to date no study investigated directly the relation between self-face perception and the electrophysiological correlates of visual awareness. Which actually are the neural correlates of consciousness, as mentioned in *Chapter I*, is a matter of continuous debate, also with regards to its electrophysiological activity (Dembski et al., 2021; Förster et al., 2020). However, there seems to be more consensus, at least in my humble view, that the Visual Awareness Negativity component might actually reflect the earliest correlate of phenomenal visual consciousness (see **Fig. 3.4**), as opposed to later components such as the P3. Is it possible that the most important and familiar object of our visual experience, as our own body, might directly influence the NCCs activity at the electrophysiological level? The perceptual and attentional prioritization characterizing self-face processing could also be reflected in the neural activity of visual awareness? That will be the focus of *Study 4*. As for *Study 5*, neuropsychology represents a unique window to approach conscious and unconscious processing. I had the chance to meet during my PhD a very rare patient, M.S., who after

surgery for the removal of a glioblastoma resulted in widespread lesions in occipito-parietal areas, which produced Hemianopia and Prosopagnosia. We conducted a study on face familiarity on M.S. to test whether face familiarity processing could be preserved despite lesions to the primary visual pathway, and at the same time to check whether covert forms of familiarity processing observed in Prosopagnosia might arise from preserved unconscious familiarity processing.

Therefore, the general aim of this chapter is twofold: on one hand, to evaluate whether the bodily self can specifically modulate the electrophysiological correlates of visual awareness, and, on the other hand, to investigate whether face familiarity processing can occur in the absence of primary visual pathway activity necessary for visual consciousness.

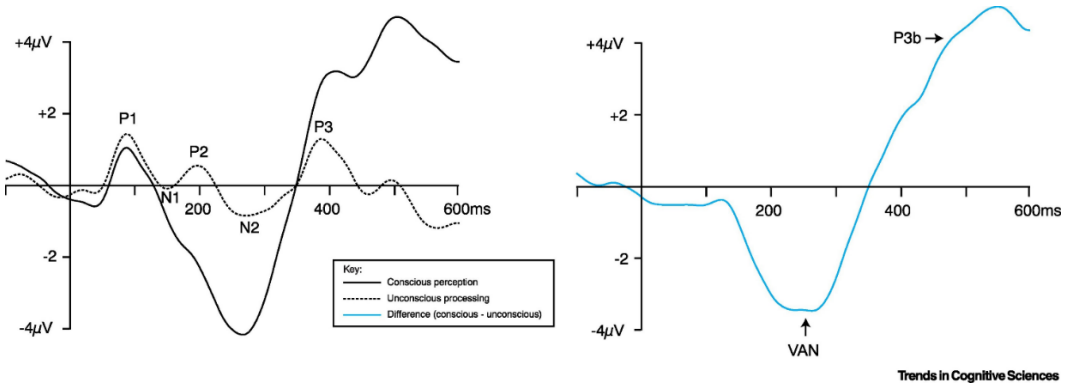

***Figure 3.4**: Representation of Event-Related Potentials within the visual domain evoked by conscious and unconscious trials. The VAN and P3 components are those usually found when contrasting (often through subtraction) the two awareness conditions from the neural signal (here represented within the PO8 EEG electrode). The image was taken from Dembsky et al., 2021.*

3.3 Study 4: **Visual Awareness Negativity is modulated by facial identity**

In Preparation

Ciorli, MacGregor, Nielsson, Kalckert & Pia

3.3.1 *Introduction*

The scientific challenge to find the NCCs (neural correlates of consciousness), defined as the minimal and jointly sufficient patterns of neuronal activation that are necessary and sufficient for a conscious state to occur, has received great interest in the last two decades, characterized by substantial disagreement by the major theories of consciousness both related to where and to when consciousness occurs (Seth & Bayne, 2022). With respect to when, a matter of debate relies on whereas electrophysiological correlates of awareness are reflected by the P3 event-related potential (ERP) component, also known as Late Potential (LP), occurring in a time window of 300-700ms after the stimulus onset in central-parietal electrodes, or are best represented by the Perceptual Awareness Negativities (PANs; Dembski et al., 2021; Förster et al., 2020), whose features vary with respect to the sensory modality in which it is investigated. Within the visual domain, the Visual Awareness Negativity (VAN) is characterized by a negative deflection on EEG amplitude in a time window range between 200-300ms in occipital-posterior electrodes, peaking at around 250ms after stimulus onset. Such characteristics might vary with respect to specific experimental conditions (Rutiku et al., 2016). In recent years a growing body of evidence dissociated the P3 from awareness, quite convincingly ruling it out as a genuine candidate as an NCC by studies finding the P3 in the absence of awareness or its presence during unawareness (Fischer et al., 2010; Schlossmacher et al., 2020, 2020; Schröder et al., 2021; Sergent et al., 2021). Such a view corroborates the stance for which P3 might reflect post-phenomenal access consciousness, whereas the earlier PAN might reflect phenomenal

consciousness (Andersen et al., 2016; Block, 1995, 2001; Derda et al., 2019; Koch et al., 2016; Koivisto et al., 2016, 2017a; Silverstein et al., 2015; Snodgrass, 2002). However, other theories of consciousness assert that the VAN rather reflects unconscious processing (i.e., the Global Workspace Theory; Dehaene et al., 2006; Mashour et al., 2020). The VAN is observed by contrasting (often through subtraction) aware and unaware trials, and it has been observed in different experiments, using a wide range of tasks such as masking (i.e., Koivisto et al., 2017b; Wilenius-Emet et al., 2004; Zotto & Pegna, 2015), binocular rivalry (Kaernbach et al., 1999), change blindness (Koivisto & Revonsuo, 2003), attentional blink (Schelonka et al., 2017), contrast manipulation (Ojanen et al., 2003), no report paradigms (for reviews, see Förster et al., 2020; Koivisto & Revonsuo, 2010).

Despite the interest in studying the relation of the VAN with awareness and attention (Bola & Doradzińska, 2021; Ciupińska et al., 2024; Doradzińska & Bola, 2023; Koivisto et al., 2005), a very few works tested how the properties of visual stimuli might influence its features. One study investigated whether stimulus size might influence the VAN properties (Eklund & Wiens, 2018), finding no evidence for an effect of such low-level features on occipital electrodes of the VAN (i.e., O1, O2). Jimenez and colleagues found that the VAN is sensitive to awareness when it pertains to simple, low-level tasks (e.g., color detection), whereas it might not be involved in tasks requiring higher-order cognitive processing (e.g., object categorization), accordingly to the 'Level of Processing' Theory (Jimenez et al., 2021) and to the finding from Kovisto et al. 2017 suggesting that the VAN is associated with conscious detection but not conscious identification (Koivisto et al., 2017b) – in other words, VAN is not influenced by higher-level processing, but rather reflects a pure form of early phenomenal conscious experience. Another important approach relies in manipulating stimulus salience, as an outstanding question relies on whereas high-level properties of stimuli might influence the VAN properties (Dembski et al., 2021). In this study we specifically investigated whether a rich and salient stimulus, specifically the self-face, might modulate the VAN component. Faces represent biologically complex stimuli very adapt to study processing outside awareness, given

the richness of information they convey engaging different cognitive systems (Axelrod et al., 2015). A fundamental aspect of face processing relies on face familiarity, which has been shown to offer clear processing advantages across various cognitive tasks (Johnston & Edmonds, 2009). Familiar faces tend to capture more attention (Jung et al., 2013; Ramon et al., 2011; Ramon & Gobbini, 2018; Visconti Di Oleggio Castello & Gobbini, 2015) facilitating quicker detection and improving accuracy during recognition tasks (Bruce et al., 2001; Burton et al., 2015; Jenkins & Burton, 2011; Natu & O'Toole, 2011). Within face familiarity, one's own face is processed with even greater efficiency, as participants show faster rection times and greater accuracy as compared to familiar faces (e.g., Devue & Brédart, 2008; Keenan et al., 1999, 2000; Sugiura et al., 2000; Tong & Nakayama, 1999), a phenomenon called self-face advantage. Indeed, the self-face is processed differently from other faces, both quantitatively and qualitatively (Alzueta et al., 2019; Apps & Tsakiris, 2014; Northoff et al., 2006; Platek et al., 2004, 2008), and a few studies showed that some aspects of self-face processing can be preserved without awareness. Indeed, the self-face is found to enjoy faster conscious access during continuous flash suppression (Geng et al., 2012; Liu et al., 2022; Zhou et al., 2020), and it attracts attentional resources when unconsciously perceived (Bola et al., 2021). Moreover, a backward masking fMRI experiment showed that unconsciously perceiving one's own face leads to the activation of the ventral tegmental area, the core of the reward system, supporting the notion that the self-face is associated with a positive reward value (Sui et al., 2015; Sui & Humphreys, 2015) even if perceived without awareness (Ota & Nakano, 2021b). The prioritization effect of the self-face both at the conscious and unconscious levels might arise from the interplay between multiple factors that are associated with one's own face perception: it entails a more robust representation, given its extensive visual experience (Tong & Nakayama, 1999; Visconti di Oleggio Castello et al., 2017; Wójcik et al., 2019) and might consequently require fewer and lower cognitive and cortical resources to be processed (Geng et al., 2012); it is associated with positive reward-values (Ma & Han, 2010b; Northoff & Hayes, 2011; Ota & Nakano, 2021b; Sui & Humphreys, 2015; Yankouskaya et al., 2017), it is enhanced at the perceptual processing level (Geng et al., 2012; Sui et

al., 2012; Ciorli et al., *under review*), it attracts attentional resources (Bola et al., 2021; Brédart et al., 2006; Devue et al., 2009; Devue & Brédart, 2008; Humphreys & Sui, 2016), and finally it is associated with multisensory information processing (Apps & Tsakiris, 2014; Bindemann, 2017; Sugiura, 2013; Tajadura-Jiménez et al., 2012). Such preferential processing before awareness has been investigated also at the electrophysiological level, for which it has been highlighted differential EEG activity within the Vertex Positive Potential component (Geng et al., 2012) and greater N2posterior-controlateral (N2PC) component (Bola et al., 2021) for the self-face compared to familiar faces. However, no study investigated whether the saliency of the self-face might modulate the earliest electrophysiological onset of visual awareness.

In sum, evidence suggests that the self-face enjoys preferential processing at the perceptual and attentional levels even before awareness. Thus, we tested whether the saliency of face stimuli might modulate the amplitude, the latency or the topography of the VAN. Furthermore, we examined whether a differential lateralized effect can be observed, considering that the right hemisphere is more tuned to self-face processing (for a review, see Molnar-Szakacs & Uddin, 2023).

3.3.2 *Methods*

Participants

18 couples of the same sex and around the same age friends were recruited, resulting in 36 participants (F = 26; mean age = 24.4 ± 4.1 years). They had normal or corrected-to-normal vision without a previous history of neurological issues and provided informed consent to participate. The study was approved by the Ethical Committee of the University of Turin (protocol n. 0486683) and performed in accordance with relevant guidelines of the declaration of Helsinki.

Stimuli and Procedure

Pictures of participants' faces were obtained in a controlled setting, with the same camera, distance and luminance conditions after the removal of, i.e., jewelry and glasses. Photos were then cropped, black/white transformed, and luminance and RMS contrast were equated through Matlab to control for low-level image features. Crucially, both the friends of each couple participated in the experiment, so each picture was used twice: as the self-face for one participant, and as the familiar face for the friend. This was made to ensure that any possible residual difference of low-level features was further controlled by distributing the (hypothetical) low-level difference within all the familiarity levels of the variables. The experiment was programmed with MATLAB (Release 2021b) and Psychtoolbox on a BenQ Monitor (1.920 x 1.080 pixel-resolution, 120 Hz, 24") at a distance of 57 cm. As for the procedure (see **Fig 3.5**), each trial started with 500ms of the fixation cross, then the target stimulus (either the self or the familiar face) was presented either on the left or the right of the fixation cross. Stimulus size was 3.8° shown at a distance of 2.2 from the center, as in (Eklund & Wiens, 2018). In the masked condition, the stimulus was shown for a very brief presentation time (i.e., 8.3/16.6/24.9/33.2/41.5ms), based on a staircase procedure that preceded the main experiment (see below), followed by the presentation of three bilateral scrambled faces for 95ms each. In the unmasked condition, the stimulus was shown for 50ms without the presentation of the masks. Then, participants were asked with a 2-forced choice task to localize the stimulus location (left/left arrow, right/right arrow), to discriminate the stimulus identity (self or familiar with top/down arrows, counterbalanced across participants), and to provide a subjective stimulus visibility 4-scale rating through the Perceptual Awareness Scale (PAS; Ramsøy & Overgaard, 2004) with the 1-4 key, in a slightly modified version: 1 corresponded to '*absolute unawareness of stimulus'*; 2 corresponded to '*awareness of stimulus location, but unawareness of stimulus identity'*; 3 reflected '*awareness of stimulus location but partial awareness of stimulus identity'*; 4 corresponded to '*clear aware experience of stimulus location and identity'*. Such change was intended to capture and disentangle awareness and unawareness of stimulus presence and the critical dimension, i.e., stimulus identity. Thus, the PAS-2 rating was nevertheless considered a subjective unconscious trial with respect to

face-identity awareness. Participants were not instructed to respond as fast as possible, but rather asked to provide the most accurate response without time limitations, and to guess if they were not aware of either stimulus identity or location. The experiment was made by 420 trials, for which in 360 trials the face stimulus was present (counterbalancing stimulus identity, location, and masked/unmasked condition, 60 trials each condition). The remaining 60 trials were catch trials, in which the face stimulus was absent within the masking condition. Before the main backward masking experiment, participants performed a staircase procedure in order to find the presentation time in which stimuli were discriminated at chance (45-55% discrimination accuracy) and stimulus visibility was below 10%. Each staircase, made of 28 masked trials, consisted of the presentation of a target face (14 self, 14 familiar trials) for a given presentation time, starting from 33ms. Participants were then asked to discriminate the stimuli and to provide subjective visibility with the PAS. If discrimination performance met the above criteria, participants used such presentation time in the main experiment; otherwise, participants repeated the staircase procedure with a lower presentation time until the criteria were met.

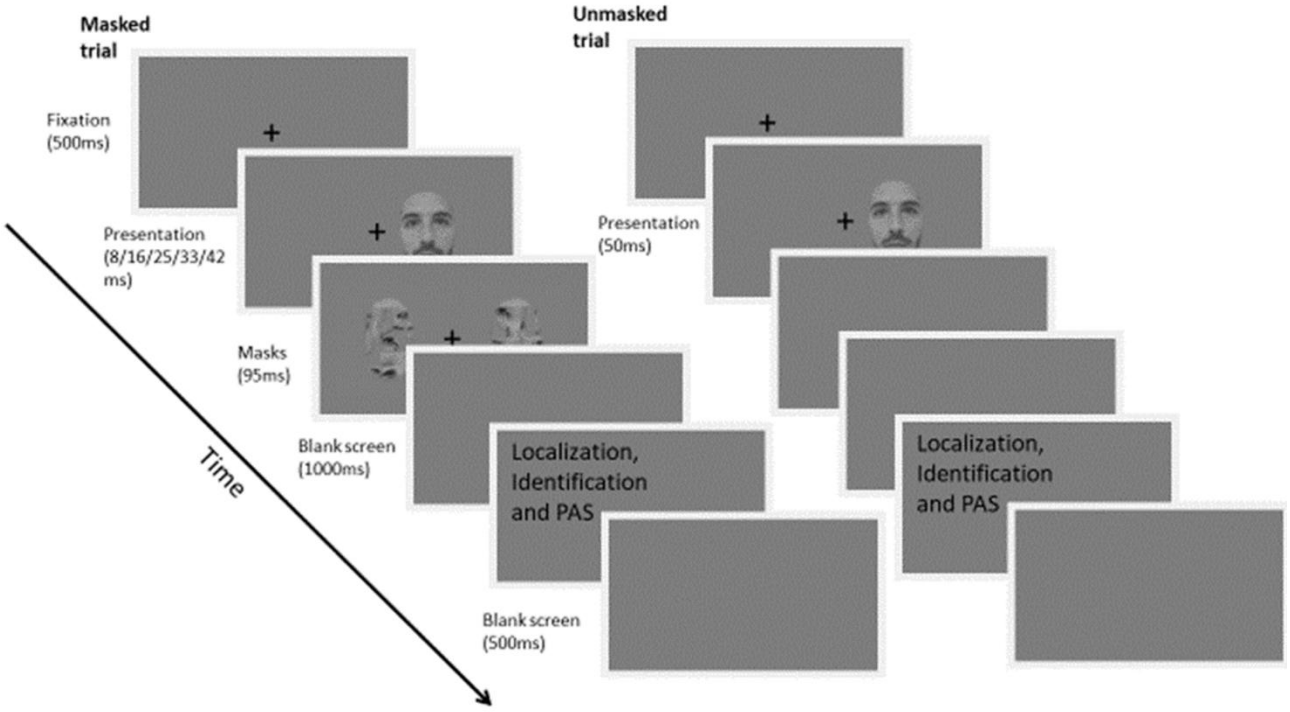

***Figure 3.5**: Schematic representation of the trial. In the masked condition, self/familiar faces were shown for a fixed presentation time (i.e., 17ms) after being calibrated in a staircase procedure, and then masked by scrambled face stimuli presented bilaterally. The unmasked condition involved 50ms of presentation time, without masks presentation. Participant were asked to perform a localization task (left/right), a discrimination task (self/familiar), and a visibility task (1-4) through the PAS.*

EEG Recording and Analysis

Brain electrical activity was recorded with 64-channel BrainAmp cap (International 10-20 system) and electrode impedances were kept below 5kΩ. The signal was amplified with the BrainAmp amplifier at a 2000Hz sampling rate. Raw EEG data were analyzed with the Brainstorm toolbox within the time domain (ERPs). The preprocessing of the data consisted in applying a Band-pass filtering (0.5-40Hz), a resample to 500Hz, and the application of the Independent Component Analysis (ICA) to remove eye blinks, saccades, and motor artifacts. Data were then re-referenced and segmented into -100 / 500ms epochs around the stimulus onset, baseline-corrected (from -200/1.5ms). Trials containing any electrode amplitude greater than 100μV or with amplitude greater than 60μV for electrodes of interest were rejected (mean trials rejected per subject: 5.2%). Bad electrodes were rejected and interpolated. Data were finally averaged across trials per condition, per subjects, and across subjects. Specifically, we averaged trials with the Self-face and trials with the Familiar face, in unaware and aware conditions, so as to have self-aware, self-unaware, familiar-aware, and familiar-unaware. Crucially, the aware condition was computed by both considering the masking condition (masked vs unmasked) or by considering the PAS scores (PAS responses = 1 and = 2, unawareness of stimulus identity; PAS responses = 3 and = 4, awareness of stimulus identity). To compute the VAN separately with respect to stimulus identity, we subtracted self-aware trials from self-unaware trials as well as familiar-aware trials from familiar-unaware trials. Grand-Average ERPs were then subjected to a rm ANOVA within the VAN time window 200-300ms after the stimulus onset with

the factors Identity (2: Self, Familiar), Hemisphere (2: Left, Right), and Area (2: Occipital, Parieto-Occipital) with a statistical threshold of .05.

3.3.3 *Results*

Behavioral Results

For the presentation times used in the main experiment, one participant met the criteria at 8ms, six participants at 25ms, and the remaining twenty-nine at 17ms. First, we analyzed the discrimination performance through the Signal Detection Theory (Stanislaw & Todorov, 1999), analyzing participants' sensitivity with the *d'* as a function of the masking or the PAS condition in order to check if participants' performance was at chance in one or both of the unconscious conditions. Discrimination-*d'* values were *d'* = .45 (± .07 SE) in the masked condition, *d'* = 2.87 (± .07 SE) in the unmasked, whereas the PAS 1-2 scores resulted in *d'* = .26 (± .05 SE), *d'* = 1.85 (± .08 SE) in the 3-4 scores. Conscious trials yielded as expected greater *d'* values within the masking ($t_{(35)}$ = 22.8, p < .001, Cohen's d = 3.85) and PAS ($t_{(35)}$ = 17.94, p < .001, Cohen's d = 3.03) conditions, indicating that discrimination performance was more accurate when stimuli were consciously perceived (see **Fig 3.6a**). A One-Sample t-test against the 0 (i.e., chance level for the *d'*) was then performed to check if unconscious *d'* were actually at chance. Results showed that, considering the masking condition, *d'* was significatively different from 0 ($t_{(35)}$ = 6.47, p < .001, Cohen's d = 1.09), and the same occurred when considering the PAS1-2 scores ($t_{(35)}$ = 4.98, p < .001, Cohen's d = .84), even if d' values were extremely low (*d'* = .45 ± .07 SE the masking, *d'* = .26 ± .05 SE the PAS). We then compared the two *d'*, which were significantly different, with the *d*' in the PAS1-2 being lower than the *d*' in the masked condition ($t_{(35)}$ = 3.84, p < .001, Cohen's d = .65). Thus, all the following analysis, both at the behavioral and EEG levels, focused on the distinction between conscious and unconscious trials considering the PAS scores.

We then analyzed the localization performance, to test whether the self-face localization *d'* was higher than the familiar face localization performance. Results showed that the two *d*' were not significantly different in the unconscious (p = .49; see **Fig 3.6b**) condition. Notably, the localization task in the conscious condition was extremely easy, for which many participants showed a ceiling effect – for such reason we did not analyze it statistically.

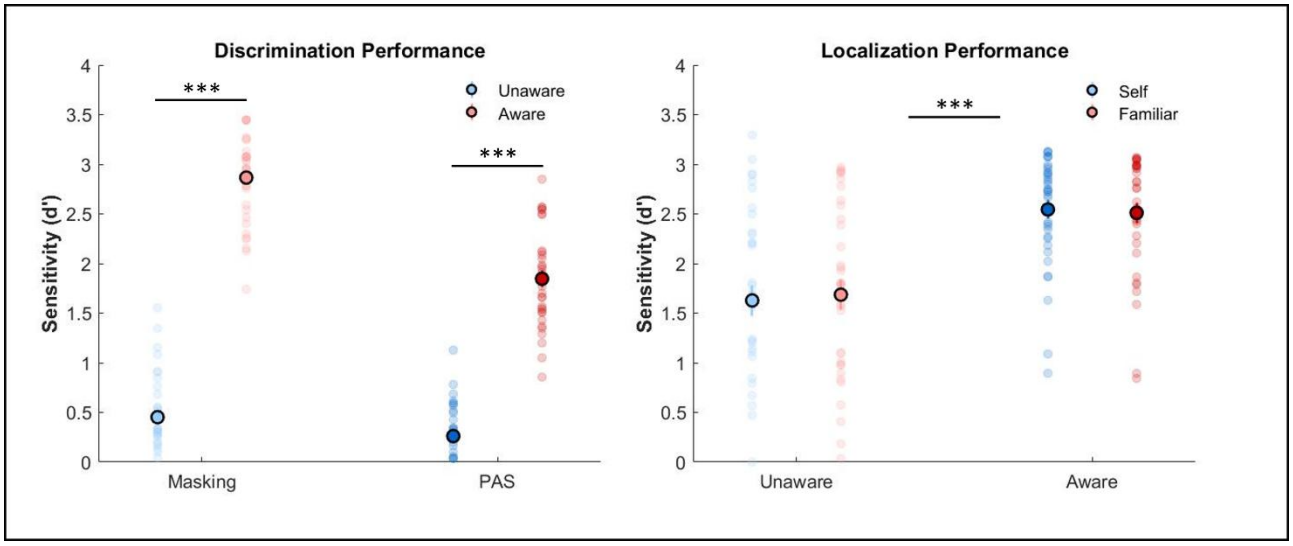

Figure 14*: a) shows sensitivity performance (d') of the discrimination task within conscious and unconscious trials, capitalized by masking (masked vs. unmasked trials, first two boxplots) and by subjective visibility (not aware vs. aware of stimulus identity, third and fourth boxplots) conditions. b) shows sensitivity of stimulus localization as a function of face identity (self/familiar) and subjective visibility ratings (PAS 1-2 vs PAS 3-4). Individual performances are plotted next to the boxplots. *p < .05, **p < .01, ***p < .001*

ERP Results

The rm ANOVA on the VAN based on PAS scores with the factors Identity (2: Self, Familiar), Hemisphere (2: Left, Right), and Area (2: Occipital, Parieto-Occipital) revealed a main effect of Area ($F_{(1,35)}$ = 11.78, p < .01, η_p^2 = .257), indicating greater VAN amplitude in parieto-occipital electrodes

as compared to occipitals ($t_{(35)}$ = 3.45, p < .01, Cohen's d = .26), and an interaction between the factors Identity and Hemisphere ($F_{(1,35)}$ = 4.97, p < .05, η_p^2 = .128). To explore the interaction, we carried post-hoc pairwise permutation t-tests (1000 permutations) with the Bonferroni correction through the Matlab toolbox Brainstorm, revealing that the VAN associated with the Self-face was more negative with respect to the VAN associated with the Familiar face only within the right hemisphere ($t_{(35)}$ = -2.87, p < .05, Cohen's d = .44) within the 250-270ms time window after the stimulus onset, despite the area. That was not the case within the left hemisphere (p > .05; **Fig 3.7**). No effects were found on VAN latency (ps > .05).

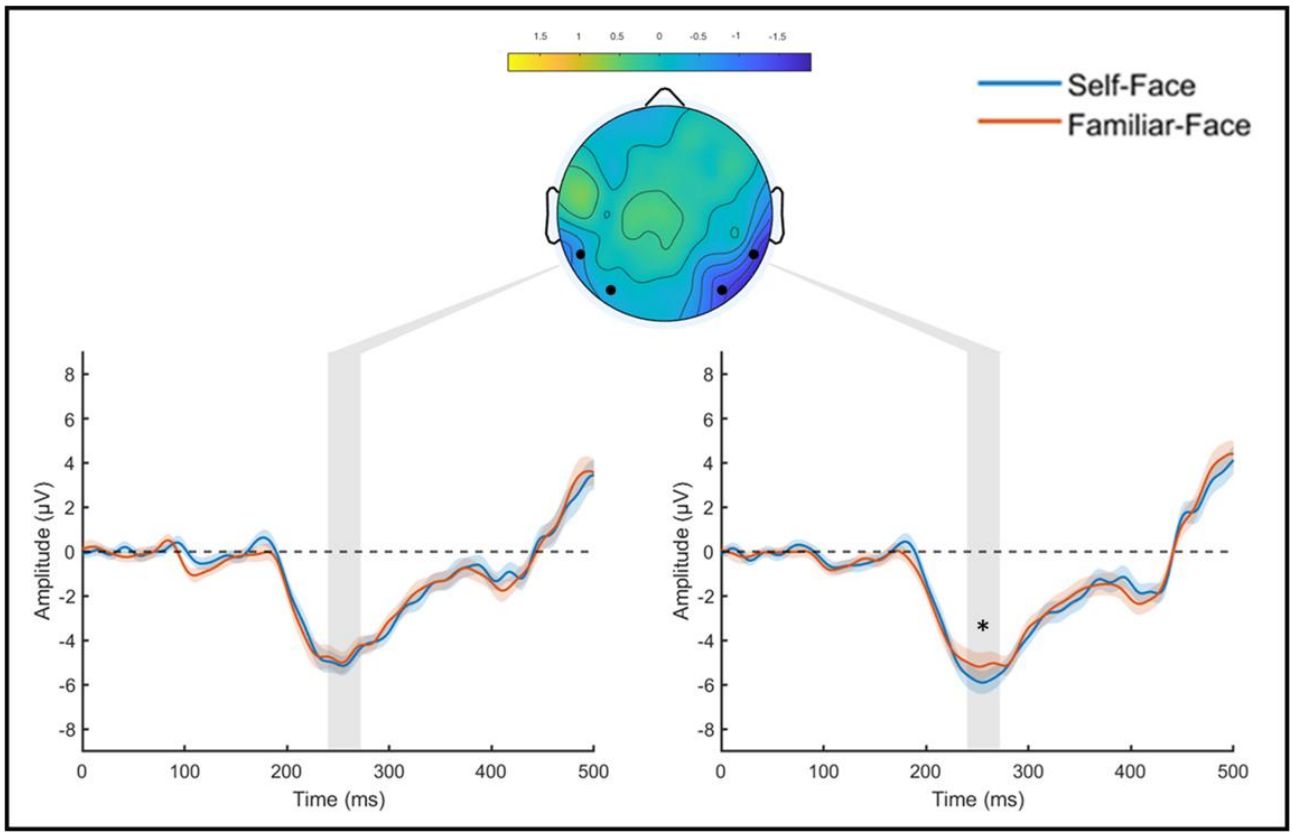

Figure 3.7*: Left) Difference waves related to aware minus unaware conditions as a function of face familiarity within the Left Hemisphere, showing the typical negativity within the 200-300 ms time range after stimulus onset characterizing visual awareness. Right) shows the same EEG response within the Right Hemisphere, for which a greater negativity amplitude characterized the Self*

*condition in the 350-270ms time range (i.e., the VAN peak). On the top, the differential topography between the self and familiar condition in the analyzed time window *p < .05*

3.3.4 *Discussion*

In this study, we tested whether stimulus high-level properties, indexed here by facial identity, might modulate the VAN component in its features. We found that the self-face, as compared to familiar faces, modulates the VAN amplitude specifically within the right hemisphere, the one mostly tuned to self-face processing.

A greater electrophysiological effect of the self-face effect is unsurprising, as numerous studies have demonstrated enhanced or differential brain activity for the self-face with respect to familiars and stranger faces (Alzueta et al., 2019, 2020; Bola et al., 2021; Estudillo, 2017; Geng et al., 2012; Wójcik et al., 2019). The self-face advantage has been observed across various paradigms, both at the conscious and unconscious levels, behaviorally and electrophysiologically. The modulation of the VAN amplitude we found might nevertheless reflect the neural prioritization of the self-face in visual awareness, potentially serving as a neural counterpart of such an enhanced effect. Two hypotheses could explain this finding.

The first hypothesis is related to the fact that the self-face entails greater activation of perceptual areas (Geng et al., 2012; Sui et al., 2012, 2015; Sui & Humphreys, 2015), leading to a 'magnification' effect that influences visual awareness processing. This may be reflected, therefore, in the enhanced VAN amplitude, consistent with studies using interocular suppression paradigms showing that the self-face is shown to break suppression faster (Geng et al., 2012; Liu et al., 2022; Zhou et al., 2020) or to dominate longer perception (Ciorli et al., *under review*). Importantly, such effects might not entail temporal efficiency of visual awareness components properties, as no effects on VAN latency were observed, but rather from perceptual signal amplification. Additionally, this effect was predominantly found in the right hemisphere, aligning with evidence from studies on

healthy individuals and split-brain patients, which highlight the specialized role of the right hemisphere in self-face processing (Keenan et al., 1999, 2001; Turk et al., 2002; Uddin, 2011; Uddin et al., 2005, 2006). The fact that we did not find any interaction between within brain areas subserving the VAN cluster might also suggests that face identity processing might influence through feedback projections lower-level visual areas (Gilbert & Li, 2013; Lamme et al., 2000; Tong et al., 2006), without being restricted to higher-level visual areas and consequently influencing the VAN cluster.

The second hypothesis involves attentional mechanisms. The self-face captures attention more effectively, both when consciously and unconsciously perceived (Bola et al., 2021; Humphreys & Sui, 2016), and heightened attentional engagement might modulate the VAN (Bola & Doradzińska, 2021; Doradzińska & Bola, 2023; Koivisto & Revonsuo, 2008; Pitts et al., 2014; Shafto & Pitts, 2015; Zotto & Pegna, 2015). Notably, the relationship between attention and the VAN has been widely investigated, albeit with mixed findings. Some theories affirm that phenomenal awareness can be dissociated from attention (Koch & Tsuchiya, 2007; Lamme, 2003; Maier & Tsuchiya, 2021) being, by definition, attentional-independent (Andersen et al., 2016; Derda et al., 2019; Koivisto et al., 2016; Koivisto & Revonsuo, 2010; Ojanen et al., 2003) – on the other side, attention can nonetheless influence awareness (Chica et al., 2010, 2011; Koch & Tsuchiya, 2007; Liu et al., 2023; Sergent et al., 2013). Indeed, for the Global Workspace Theory attention is a prerequisite for conscious access (Dehaene, 2001b; Dehaene et al., 2006). Distinguishing between attentional ERP components and the VAN is challenging as, for instance, the Selection Negativity (SN; Mangun, 1995) and the N2pc (Eimer, 1996) occur within similar timeframes as the VAN but are nevertheless computed differently: the VAN is observed when contrasting aware versus unaware trials, whereas the SN when contrasting task-relevant versus task-irrelevant stimuli, and the N2pc when comparing contralateral stimuli processing. Despite these nuances, studies exploring the dissociation between awareness and attention have produced conflicting results, some supporting the fact that the VAN might be closely related to selective attention (Koivisto & Revonsuo, 2008; Pitts et al., 2014; Shafto & Pitts, 2015;

Zotto & Pegna, 2015), some supporting its independence (Bola & Doradzińska, 2021; Ciupińska et al., 2024). Thus, it is plausible that the observed modulation of the VAN amplitude in our study could reflect enhanced attentional mechanisms triggered by self-face processing. Indeed, Ota and Nakano (2021) suggested that dopaminergic activity associated with self-face processing without awareness might trigger a greater engagement of attentional resources and the consequent self-advantage (Ota & Nakano, 2021b). Intriguingly, in this study such modulation was only observed within the right hemisphere and not bilaterally, even if stimulus location was counterbalanced, for which attentional ERPs like the N2PC are highly sensitive.

Finally, we did not find any advantage of the self-face at the behavioral level (i.e., enhanced localization), something one would not expect given the differential brain activity we found. Interestingly, this is in line with two imaging studies that investigated unconscious self-face processing. Bola et al., (2021) found greater N2PC responding to the self-face in a dot-probe masking experiment, but not associated with faster reaction times for the probe when congruent with the self-face location (Bola et al., 2021) – similarly, Ota and Nakano found greater involvement of the dopaminergic pathway after unconscious presentation of the self-face in the absence of behavioral advantages (Ota & Nakano, 2021b). The only studies finding behavioral advantages of self-face manipulating awareness are those using the bCFS paradigm (Geng et al., 2012; Liu et al., 2022; Zhou et al., 2020), possibly entailing methodological differences in the stimulus processing assessment. By contrast, supraliminal studies are very sensitive to behavioral advantages of the self-face.

To summarize, our results show that high-level stimulus saliency, capitalized here by facial identity, modulates the VAN amplitude, as a consequence of enhanced perceptual processing or enhanced attentional resources allocated to the self-face, and providing, in our knowledge, the first evidence for the effect of high-level stimulus content on the earliest electrophysiological correlate of visual consciousness. However, some limitations must be observed before concluding. First, the discrimination *d'* for unconscious trials was slightly above the chance level, even if very low (i.e., *d'*

= .45). This means that trials were not objectively unaware, possibly allowing for partial and degraded awareness of stimulus processing, or a blindsight-like performance (Dehaene & Changeux, 2011; Overgaard et al., 2006), not convincingly ruling out conscious traces (Holender, 1986; Newell & Shanks, 2014; Schmidt, 2015). Even if presentation times were individually assessed by a staircase procedure and the experiment randomized masked and unmasked trials, the large number of trials might have induced habituation over visual sensitivity stimulation. For that reason, all unaware trials were considered through subjective measures of awareness, as a standard of consciousness studies, but known to be prone to response biases and subjective criteria (Persuh, 2018). However, even subjective unaware discrimination performance was slightly above the chance level, even with a smaller *d'* (*d'* = .26) Second, to better assess the role of attention on the effect of the self-face on the VAN, directly manipulating participants' attention through attended and not attended trials would have deepened the interplay between facial identity, attention and visual awareness. Future studies might indeed tackle this issue and explore whereas this effect might be driven by attentional or perceptual mechanisms.

3.4 Study 5: **Unconscious face familiarity processing in a patient with Hemianopia and Acquired Prosopagnosia: A Single Case Study**

In Preparation

Ciorli[+], Camassa Nahi[+], Villa, Celeghin & Pia

3.4.1 *Introduction*

As previously discussed in this thesis, the ability to recognize people's identity is a fundamental skill crucial for social behavior. This skill, which is typically automatic and highly intuitive, is impaired in individuals affected by prosopagnosia, a selective visual agnosia characterized by significant deficits in face recognition and selective impairments in conscious discrimination of individual faces (Bodamer, 1947). Prosopagnosia is a very heterogeneous condition that can be classified as acquired, as a consequence of brain damages, or congenital/developmental, being present since birth without evident brain lesions (Behrmann & Avidan, 2005; Duchaine & Nakayama, 2006), and in apperceptive or associative variants, characterized by deficits in either structural face encoding or in face-semantic associations, respectively (Dalrymple et al., 2014; De Renzi et al., 1991; Liu et al., 2021). Interestingly, some prosopagnosic patients, in the absence of overt face discrimination, might exhibit forms of covert face recognition (Bruyer et al., 1983), as differential physiological (Bauer, 1984; Bobes et al., 2004; Renault et al., 1989; Tranel & Damasio, 1985) or enhanced behavioral (Bate et al., 2009; Bruyer et al., 1983; De Haan et al., 1991; De Haan et al., 1987; Rivolta et al., 2012; Young et al., 1988) responses to familiar faces despite lacking conscious recognition, suggesting preserved unconscious face familiarity processing. However, in prosopagnosia stimuli are consciously perceived – what it's unconscious is the semantic feature related to face identity. Thus, it remains unclear whether this covert recognition arises from actually

preserved unconscious face processing or whether residual cortical processing and awareness of the stimulus itself is required for such implicit processing. Covert face recognition in prosopagnosia likely stems from preserved emotional responses to faces, mediated by subcortical structures through direct connections between FFA and the amygdala (Breen et al., 2000; Nagai, 2007), being unaffected in Prosopagnosia. These structures receive inputs from cortical face-processing areas allowing for emotional associations, as opposed to the deficits observed in Capgras syndrome, characterized by spared identity processing with impaired emotional associations (Ellis & Lewis, 2001). However, other evidence showed that face-emotional processing might be also cortico-independent, with subcortical structures receiving direct inputs from the retina (Harting et al., 1991; Lyon et al., 2010) and being capable of fast and coarse face processing (Johnson, 2005). This raises an intriguing question: could emotional face processing associated with face familiarity (rather than face expressions) occur without cortical involvement in the absence of awareness?

Studies on hemianoptic patients historically provided evidence for processing in absence of visual awareness. Hemianopia arises after brain damages to primary visual areas, resulting in cortical blindness in the part of the visual field topographically corresponding to the damaged portion of V1. Despite the lack of conscious visual awareness in the affected field, some hemianoptic patients, termed blindsight (Humphrey & Weiskrantz, 1967; Weiskrantz et al., 1974), showed some residual visual processing abilities. For instance, blindsight patients can explicitly discriminate specific visual features of stimuli presented in the blind field above the chance-level, such as shapes, motion and emotional expressions (for a review, see Cowey, 2010) despite cortical blindness. The ability of blindsight patients to process emotional faces, called ‘affective blindsight’ (De Gelder et al., 1999; Heywood & Kentridge, 2000), has been extensively documented in the literature (for reviews, see Celeghin et al., 2015; Diano et al., 2017; Tamietto & de Gelder, 2010) highlighting an important role of emotional perception for survival – that is, having an unconscious rapid system for detection of emotionally salient stimuli (i.e., fearful faces) could trigger adaptive responses to environmental

stimuli (Alpers & Pauli, 2006; Öhman, 2002; Öhman & Mineka, 2001; Tamietto & de Gelder, 2010; Vuilleumier & Driver, 2007). Neuroimaging studies investigating the neural mechanisms behind unconscious processing in blindsight suggested a crucial role of the subcortical pathway, often referred as a 'low, fast and coarse' route, with the main purpose of having a rapid response to salient stimuli, as opposed to the 'high, slow and fine' cortical conscious route aimed to have a complex and integrated evaluation of environmental stimuli (LeDoux, 1998b). This lower pathway, involving structures like the superior colliculus, the pulvinar and the amygdala (LeDoux, 1998b; Morris, 2001), enables detection of faces and their emotional content, without conscious awareness, in less than 100ms (Maior et al., 2010; Nguyen et al., 2014, 2016).

In healthy subjects, but also in prosopagnosic patients, subcortical structures might similarly support preserved unconscious and covert emotional responses to faces. Evidence from neuroimaging studies showed that subcortical structures such as the amygdala, nucleus accumbens and VTA differentially respond to face identity (Oikawa et al., 2012; Ota & Nakano, 2021a; Schwartz et al., 2003; Ueno et al., 2014) even during masking (Ota & Nakano, 2021b). Moreover, face familiarity has been found to influence visual awareness, with faster access to consciousness as a function of familiarity (Geng et al., 2012; Gobbini et al., 2013). A recent study attempted to simulate the covert recognition mechanisms observed in prosopagnosia using Continuous Flash Suppression (CFS) in neurotypical participants. The researchers found that when familiar faces were suppressed by CFS, pupil responses - a reliable index of implicit emotional arousal - differed depending on whether the suppressed face was familiar or unfamiliar. The authors concluded that the emotional discrimination observed in prosopagnosia might stem from preserved unconscious face-processing mechanisms, allowing facial familiarity discrimination (Mejía et al., 2024).

To further investigate this hypothesis, we examined face familiarity processing in a single case study involving patient M.S. Following surgery for the removal of a Glioblastoma, M.S. sustained extensive occipito-parietal damages, resulting in hemianopia, and reported a persistent

deficit in face perception. The neuropsychological evaluation revealed significant difficulties in face processing, consistent with Acquired Prosopagnosia. Prior to her passing, we conducted the present study which first included a comprehensive neuropsychological assessment followed by an experimental paradigm, to explore unconscious face familiarity processing through the Redundant Target Effect (RTE). The RTE relies on a visual paradigm in which stimuli are presented either unilaterally (within the intact or blind portions of the visual field) or bilaterally (simultaneously in both fields). Participants are instructed to respond as quickly as possible to the presence of any stimulus. Both healthy individuals (Tamietto & De Gelder, 2008) and blindsight patients (De Gelder et al., 1999, 2001, 2002, 2002; Tamietto et al., 2009) respond faster to bilateral stimuli than to unilateral stimuli when one stimulus is unconsciously perceived (Celeghin, De Gelder, et al., 2015; Celeghin, Savazzi, et al., 2015; Corbetta et al., 1990; Leh et al., 2010; Marzi et al., 2009; Tamietto & de Gelder, 2010; Tomaiuolo, 1997) - a phenomenon attributed to hemispheric summation effects. However, even if such summative effects are absent in hemianoptic patients without blindsight possibly as a consequence of specific differential visual system reorganization at the extrastriate and subcortical levels that can differ between patients (Bertini et al., 2013), they nevertheless show implicit processing of stimuli in the blind field. Specifically, modified versions of RTE including semantic manipulations can be used to evaluate congruency or incongruency effects on bilateral stimulus performance. For example, studies using the RTE with emotional faces (i.e., happy vs. fearful) found that hemianoptic patients responded faster to happy faces presented in their intact field *only* when a fearful face was simultaneously presented in their blind field, even in the absence of blindsight-like visual skills (i.e., without above-chance discrimination in explicit tasks or implicit summative RTE; Bertini et al., 2013, 2019; Cecere et al., 2014). These results provided evidence for unconscious emotional processing in hemianoptic patients, being possibly mediated by the subcortical visual pathway involving the superior colliculus, pulvinar, and amygdala (Liddell et al., 2005; Morris, 2001; Morris et al., 1998, 1999; Vuilleumier et al., 2003; Whalen et al., 1998, 2004; Williams, Das, et al., 2006), as the primary retino-geniculo-striatal visual pathway is significatively

targeted only when stimuli are consciously, rather than unconsciously, perceived (Diano et al., 2017; Pasley et al., 2004; Williams, Das, et al., 2006; Williams, Liddell, et al., 2006). Moreover, such effect seems to be preserved only in patients with left-hemisphere lesions, suggesting a crucial role of the right-hemisphere subcortical pathway for unconscious affective stimuli processing (Bertini et al., 2019; Cecere et al., 2014; Gainotti, 2012). Interestingly, the right hemisphere seems to be involved also in face familiarity processing (Negro et al., 2015; Ota & Nakano, 2021a; Sugiura et al., 2000; Uddin et al., 2005).

Upon such considerations, in this study we manipulated face identity in a RTE task with three aims. The first was to assess any blindsight-like skills in patient M.S. by investigating unilateral vs bilateral summation effects. The second was to assess implicit covert familiarity processing considering the patient's Prosopagnosia in the RTE unilateral conditions involving familiar/other faces. Finally, the third aim was to investigate whether the experimental performance would differ concerning face familiarity *regardless* of the visual field (i.e., presented in the intact or blind hemifield), as in the above-mentioned studies (Bertini et al., 2013, 2019; Cecere et al., 2014). If so, that would provide evidence for the possible cortico-independent involvement of subcortical structures in face familiarity processing, considering that a patient suffering from both Acquired Prosopagnosia and Hemianopia after a left occipito-parietal lesion would possibly represent the worst scenario for cortical visual processing of face identity.

3.4.2 *Methods*

M.S. Clinical History

M.S. was a 74-year-old, right-handed woman with 13 years of formal education. In December 2022, she was admitted to the neurology department for the first time because she had gait disturbances due to visual disturbances. MRI revealed a large contrast-enhancement lesion in the left

occipital lobe with a central necrotic area. Perfusion imaging showed an elevated rCBV, suggesting a high-grade glioma. As a results, the patient underwent brain surgical in January 2023. The neuropathological analysis of tumors revealed Glioblastoma WHO grade 4 in according to the fifth edition of the WHO classification of Tumors of the Nervous System (Louis et al., 2021). No complications occurred after surgery. Ophthalmological examination disclosed a right homonymous hemianopia (see **Fig. 3.8**). Following the Declaration of Helsinki, patients provided written informed consent to participate in the study, approved by the Ethical Committee of the University of Turin (protocol n. 0486683).

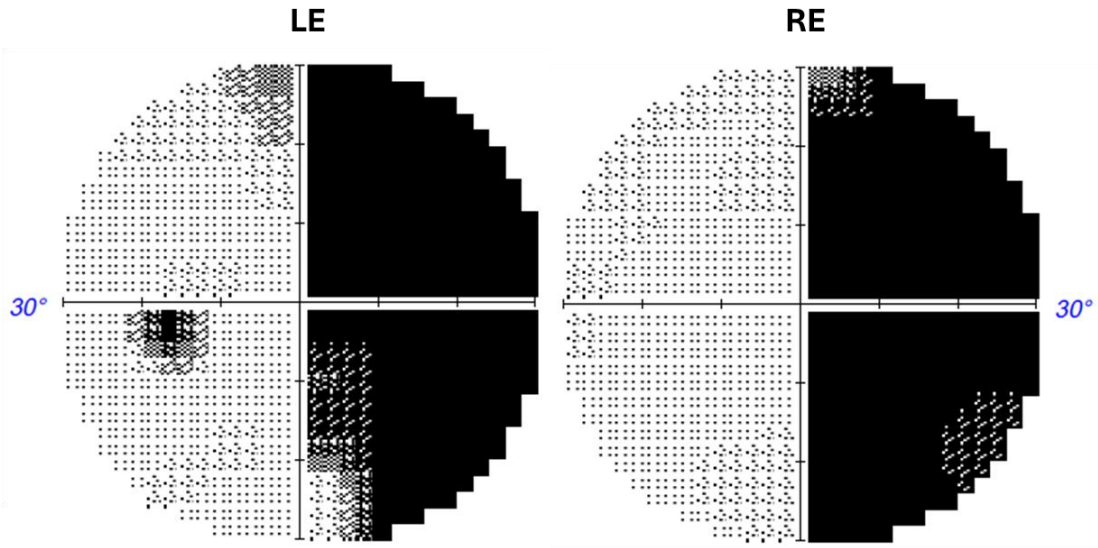

Figure 3.8*: Automated visual perimetry of patient M.S. (Carl Zeiss Meditec, Inc). Axial hash marks indicate 10 visual degree increments. LE, left eye; RE, right eye.*

Neuropsychological assessment

Patient M.S. underwent a neuropsychological evaluation, about one month after the surgical intervention and before the beginning of neuro-oncologic treatment. She reported post-surgical

difficulties in visuo-motor coordination, reading eye movement control and face perception, including recognizing her own face in the mirror. She described faces as appearing distorted, likening them to a "Picasso paintings". Face recognition was partially facilitated by contextual cues and auditory input, such as recognizing the person's voice.

During the anamnestic interview and test administration, the patient was cooperative, and her behaviour was appropriate to the situation. Vigilance and sustained attention were normal. The patient was oriented in the personal, time and space dimensions. The language was fluent in the absence of aphasic disturbance. Verbal auditory and written comprehension were preserved.

The first level evaluation of cognitive status, conducted through the administration of the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005), revealed preserved global cognitive functioning with a normal global score. No impairment of language, memory and attention emerged during the test.

The second level in depth evaluation focused on visuo-spatial and visuo-perceptive abilities based on the patient's reported symptoms (see **Table 1**).

Visuospatial exploration abilities were assessed using the *Line Cancellation Test* (Spinazzola et al., 2010), which revealed no asymmetry in spatial exploration but reduced accuracy in exploring the contralesional space probably due to a visual field deficit not yet compensated. Furthermore, the administration of the Line Bisection Test (Spinazzola et al., 2010) highlighted a deviation of the midpoint towards the right contralesional space that we interpret as a *hemianoptic error* in accordance with Zihl et al., 2009. Visual-spatial abilities were further assessed using the *Visual Object and Space Perception Battery* (VOSP; Warrington & James, 1991). Visual acuity and shape discrimination abilities were normal, as demonstrated by the performance on the *Shape Detection Screening Test*. The patient demonstrated difficulties in tasks evaluating the ability to localize dots in space (Dot Counting), and to perceive the spatial position of an object in a two-dimensional space (Position Discrimination, Number Location). Complex spatial perceptions were also impaired, as shown by the

cube analysis task, which required interpreting a two-dimensional representation in three-dimensional space (cube analysis).

A qualitative test involving geometric drawing in coping highlighted the patient's ability to perceive the basic properties of shapes and maintain visuo-motor coordination for simple two-dimensional drawings. However, the reproduction of a three-dimensional geometric figure (Cube) revealed impairments in visuo-spatial analysis.

Elementary visuo-perceptive abilities required for object recognition were assessed using the VOSP. The patient achieved a borderline score on tasks requiring the identification of degraded letters (Incomplete Letters) and the recognition of object shapes presented among distractor stimuli (Object Decision). Performance was normal for tests involving the identification of silhouettes of objects and animals from unusual perspectives (Silhouettes) and the progressive identification of silhouettes (Progressive Silhouettes).

Visual object recognition abilities were assessed using the *Associative Match Task* (part of the Birmingham Object Recognition Battery), where the patient was capable of accessing semantic knowledge and correctly identifying objects.

A qualitative evaluation of the patient's ability to access semantic-structural knowledge about colours did not reveal any impairments at this level of processing.

A face/non-face decision task was employed (Test di Decisione Fisionomica; Della Sala et al., 1995). to investigates the ability to access the subject's knowledge of the essential components of a facial pattern (Della Sala et al., 1995) . The patient obtained a borderline score in this test, highlighted the presence of fragilities in processing the structural features of faces. The administration of a qualitative test for the recognition of famous faces revealed preserved abilities in visual recognition and access to verbal information for naming. However non facial features might have cued the patient in facial

recognition. A standardized test, Cambridge Face Memory Test (CFMT; Duchaine & Nakayama, 2006), was administered to assess identity recognition of unfamiliar faces. The CFMT requires identifying six familiar faces across three phases: recognizing identical images; recognizing the same faces in different images with varying viewpoints and/or lighting conditions; and recognizing the same faces in different images obscured by visual noise. The patient showed difficulty in ordering a series of faces based on their similarity to a target face, where the comparison stimuli are gradually altered to resemble several different faces to varying degrees. The accuracy of the response was 57% (cut-off: 60%).

In conclusion, the neuropsychological evaluation confirmed that the patient exhibited impairments in face perception, with the deficit appearing to stem from apperceptive difficulties. Additionally, difficulties in visuo-spatial analysis were also observed. Visual-perceptive abilities and object recognition were preserved, although some fragilities were noted in the recognition of object shapes.

Table 1.

TEST	Raw score	Adjusted* score	Cut-off	Description
Montreal Cognitive Assessment (MoCA, v. 8.1, Aiello et al., 2021)	21	21.20	18.58	Normal
Line Cancellation Test (Spinazzola et al., 2010)	34	-	34	Borderline
Line Bisection Test (Spinazzola et al., 2010)	5	-	7	**Impaired**
The Visual Object and Space Perception Battery (VOSP, Warrington et al., 1991)				
Shape Detection Screening Test	19	-	15	Normal
Incomplete Letters	16	-	16	Borderline
Silhouettes	19	-	15	Normal
Object Decision	13	-	14	**Impaired**
Progressive Silhouettes	15	-	15	Borderline
Dot Counting	5	-	8	**Impaired**
Position Discrimination	9	-	18	**Impaired**
Number Location	2	-	7	**Impaired**
Cube Analysis	2	-	6	**Impaired**
Birmingham Object Recognition Battery (BORB)				

Associative Match Task	30		22	Normal
Test di Decisione Fisionomica (Della Sala et al., 1995)	16		16	Borderline
Cambridge Face Memory Test (Duchaine & Nakayama, 2006)	57		60	**Impaired**

*Row scores have been converted in to adjusted scores according to Italian norms based on age and education

Lesion Mapping Analysis

The neuroimaging acquisitions after the surgical removal were performed on a 1.5T SIGNA Voyager scanner (GE Healthcare, Italy). Acquisition procedure includes T1w structural images (Slice Thickness = 1.2 mm; Echo Time = .012188; Repetition Time = .5s; Flip Angle = 90°) and a 3D FLAIR (Fluid Attenuated Inversion Recovery) sequence (Slice Thickness = 1.6 mm; Echo Time = .116424; Repetition Time = 6.5s; Flip Angle = 90°). Lesion mapping was performed defining the lesion burden and isolating white and grey matter hyperintensities from the post-surgical FLAIR MRI. AFNI (Cox, 1996) and FSL (Jenkinson et al., 2012) has been used for lesion visualization and final mask correction. The final lesion map was registered to the standard MNI152 template using the matrix (*3dNwarpApply*) derived from the non-linear registration of T1 structural image (*3dQwarp*).

The lesion was located entirely in the left hemisphere, and it is graphically represented in MNI space in **Fig 3.9A**. The lesion consists in two clusters of 40224 and 2817 voxels each, whose center of mass is located in MNI coordinates X = -22.5; Y = -69.5; Z = 26.2 and X = -19.8; Y = -93.6; Z = -10.5 respectively. Overlap between the lesion and the Eickhoff Zilles macro labels from the MNI N27 Atlas, available in AFNI, indicated that the first cluster is located in the Middle Occipital Cortex (32% of the cluster), Superior Occipital Gyrus (20% of the cluster), Superior Parietal Lobule (17% of the cluster), Calcarine gyrus (13% of the cluster), Cuneus (6% of the cluster), Precuneus (5%

of the cluster), Inferior Parietal Lobule (2%), Lingual gyrus (1%) reaching in less than 1% areas such as Postcentral gyrus, Angular gyrus, Middle Temporal gyrus and Fusiform gyrus. The second cluster, more inferiorly positioned, overlaps with Lingual gyrus (43%), Inferior Occipital gyrus (31%), Calcarine gyrus (18%), Middle Occipital gyrus (4%) and Fusiform gyrus (1%).

Disconnectome

Normalized brain images and the lesion mask were used to estimate the probability of white matter tract disconnection by comparison with tract atlases. This method, validated in previous studies (e.g., Foulon et al., 2018), was implemented in the BCB toolkit and is currently applied to investigate white matter tract disconnection following neurological damage (e.g., Dulyan et al., 2022; Pacella et al., 2019, 2020). Consistent with prior research (Foulon et al., 2018), only probabilities greater than 50% were considered indicators of white matter tract disconnection. Graphical representation of Disconnectome is presented in **Fig 3.9B**. Disconnected tracts, expressed in percentages indicating the chance to have fiber disconnected in the tract, are Cingulum left (100%), Cingulum anterior (100%) and Posterior (93%), Corpus callosum (100%), left Inferior Frontal fasciculus (100%), left Inferior Longitudinal fasciculus (100%), left Optic Radiation (100%), Superior Longitudinal Fasciculus II Left (99%), Superior Longitudinal Fasciculus III Left (56%), Inferior Fronto Occipital Fasciculus Left (96%), Frontal Commissural (82%), Arcuate Long Segment (66%).

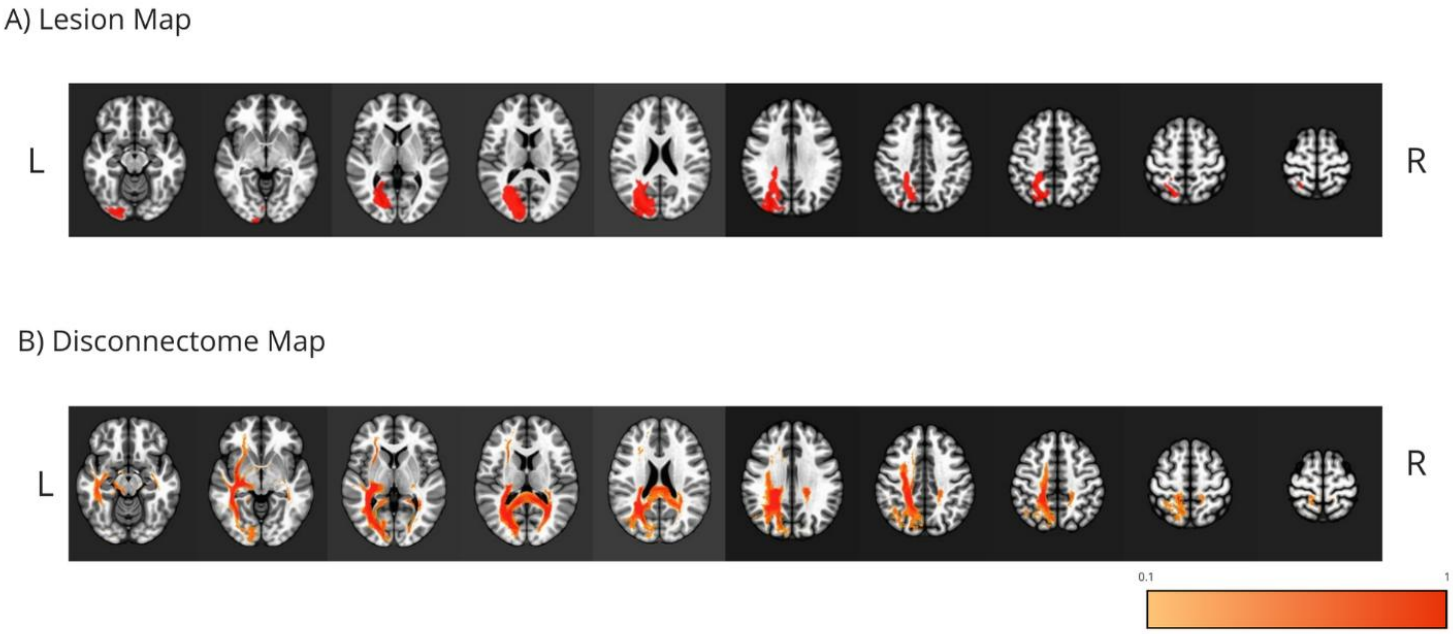

Figure 3.9*: A) Axial view of patient's lesion mask registered in MNI152 space. B) Axial view of Disconnectome in MNI152 space.*

Redundant target task

Apparatus and Stimuli. The patient's caregiver, in this case her daughter, came with MS to the laboratory, where her face was photographed and cropped with Photoshop. A same-gender and around the same-age participant photo, acquired in the same settings, was picked as another stimulus. Stimuli were then cropped with Photoshop, b/w transformed, and subjected to a scramble manipulation in order to have stimuli exemplars with the same low-level features but disrupted high-level semantics. The patient was asked to lay with the head on a chinrest placed at 57cm from a BenQ Monitor (1.920 x 1.080 of pixel resolution, 120 Hz, 24"). Ocular behavior was measured with the eye tracker Eye-Link 1000 HR at a sampling rate of 120Hz, managed with the experiment programmed with Matlab on a grey background. Precisely, after an eye-calibration phase, the patient was asked to maintain a constant fixation on the central fixation cross (1.5°) within an area of interest of 2.5°.

Trials in which patient's gaze was out of the area of interest were discarded and repeated online. Stimulus' size and position were adjusted with respect to the patient's blind field, resulting in 8x8° at a horizontal distance of 7° between the stimulus center and the fixation cross, on the right within the blind field, on the left for the intact field.

Procedure. Each trial began with a jittered inter-trial interval between 1200-2200ms. Then, the presentation of stimuli occurred for 300ms. Stimuli could be presented unilaterally, within the blind or the intact field, or bilaterally, in a congruent or incongruent manner (see **Fig 3.10**). After the stimulus presentation, there were 1500ms for the response. The patient was instructed to respond as fast as possible whenever she perceived a stimulus, irrespective of its features. After 1500ms, a new trial began. Stimuli were the familiar face, the other face, and their scrambled versions. All conditions were counterbalanced, with the exception that scrambled faces were only presented either unilaterally in the intact (to account for conscious effects of low-level stimulus properties on RTs), either bilaterally in the blind field (to account for unconscious effects of low-level stimulus properties on RTs of the stimulus in the intact field). The total number of trials was 240, and the experiment lasted around 20 minutes, with two breaks in between for eye-resting.

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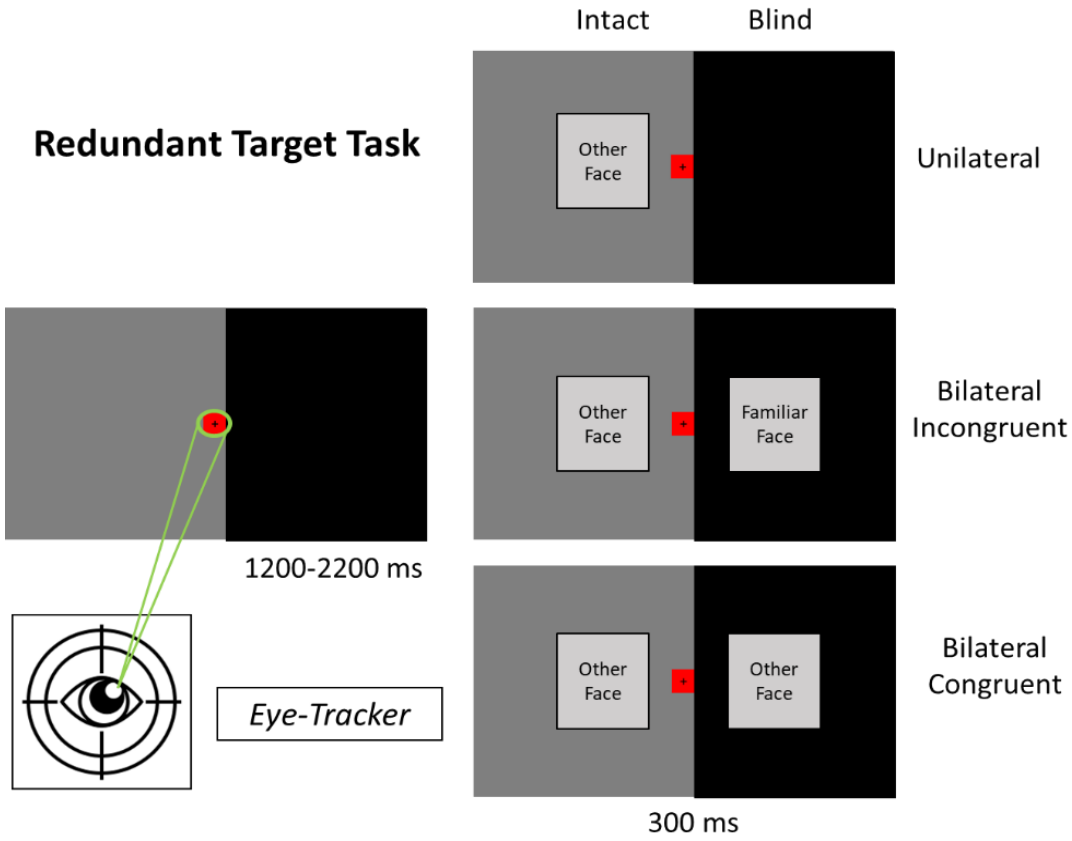

***Figure 3.10**: Schematic representation of the trial. After an ITI around 1200-2000 ms, the patient was exposed to either unilateral, bilateral congruent, or bilateral incongruent stimuli presentation (familiar, other, scrambled-familiar, scrambled-other faces) for 300ms. The eyetracker continuously monitored the patient's gaze that had to be focused on the fixation-cross area of interest. The patient was asked to press the space bar as soon as she perceived any stimulus.*

3.4.3 *Results*

As data were not normally distributed (Shapiro-wilks results), following analysis on single trials per condition followed nonparametric tests. The patient never responded to unilateral stimulus presentation within the blind visual field, indicating that the stimulus location was correct. To assess the presence of the summation effect in the RTT, we compared, with a paired sample t-test, mean responses of unilateral conditions (mean = 512ms ± 10 SE) with responses of bilateral conditions (mean = 505ms ± 8 SE). The comparison was not significant (p = .93). As for the presence of covert

familiarity processing for prosopagnosia, we then performed a t-test between unilateral familiar-face (mean = 480ms ± 14 SE) and other-face (mean = 520ms ± 19 SE) conditions within the intact field. Results showed a trend for significance (z = 1.48, p = .076, r = .43), as the familiar-face responses were faster than other-face responses but not enough to reach statistical significance. In addition, the same comparison between the unilateral scrambled versions of the two stimuli in the intact field was not significant (p = .51), with almost identical mean responses. See **Fig 3.11**.

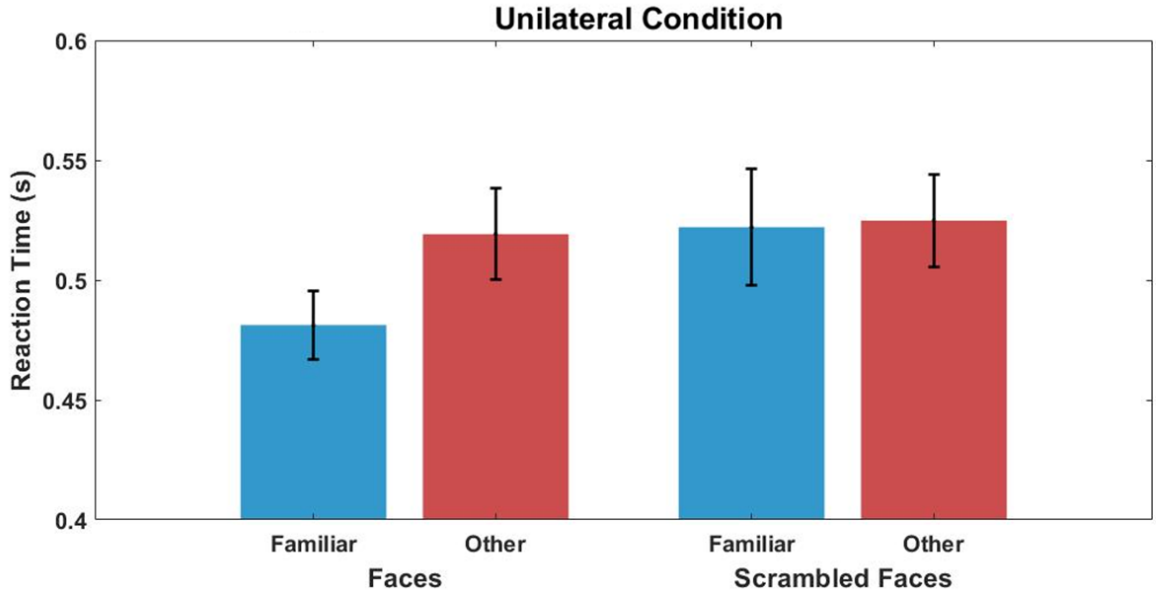

Figure 3.11*: Results from the unilateral conditions only in the intact visual field (seconds ± SD). *p < .05, **p < .01, ***p < .001*

Then, we conducted two one-way repeated measures ANOVA within the three conditions in which either the familiar or the other faces were presented in the *intact field*: in other words, in the first ANOVA the factors were unilateral – familiar (F), bilateral/incongruent familiar (F-o, uppercase letters indicate intact, lowercase blind), bilateral/congruent familiar (F-f); the second ANOVA was identical but with respect to the other face presented within the intact field (i.e., O; O-f; O-o). The familiar one-way ANOVA was not significant (p = .78; see **Fig 3.12**), suggesting that there were no

effects of unilateral vs bilateral conditions, nor between their congruences. In contrast, the other one-way ANOVA showed a main effect of condition ($\chi 2$ = 10.53, p < 0.01, W = .35). Post-hoc comparisons revealed a significant decrease in reaction times in the only condition in which the familiar face was presented (i.e., in the blind field), both as compared to the other-unilateral (z = 2.38, p < .01, r = .7) and to the other-bilateral congruent (z = 1.68, p < .05, r = .43) condition. Crucially, this significance disappears if we consider the same ANOVA but with the scrambled familiar face in the blind field (i.e., O-f scrambled; p = .42). These results suggest that the perception of the familiar face, either in the intact of the blind field, speeded the response of the patient despite Hemianopia and Acquired Prosopagnosia.

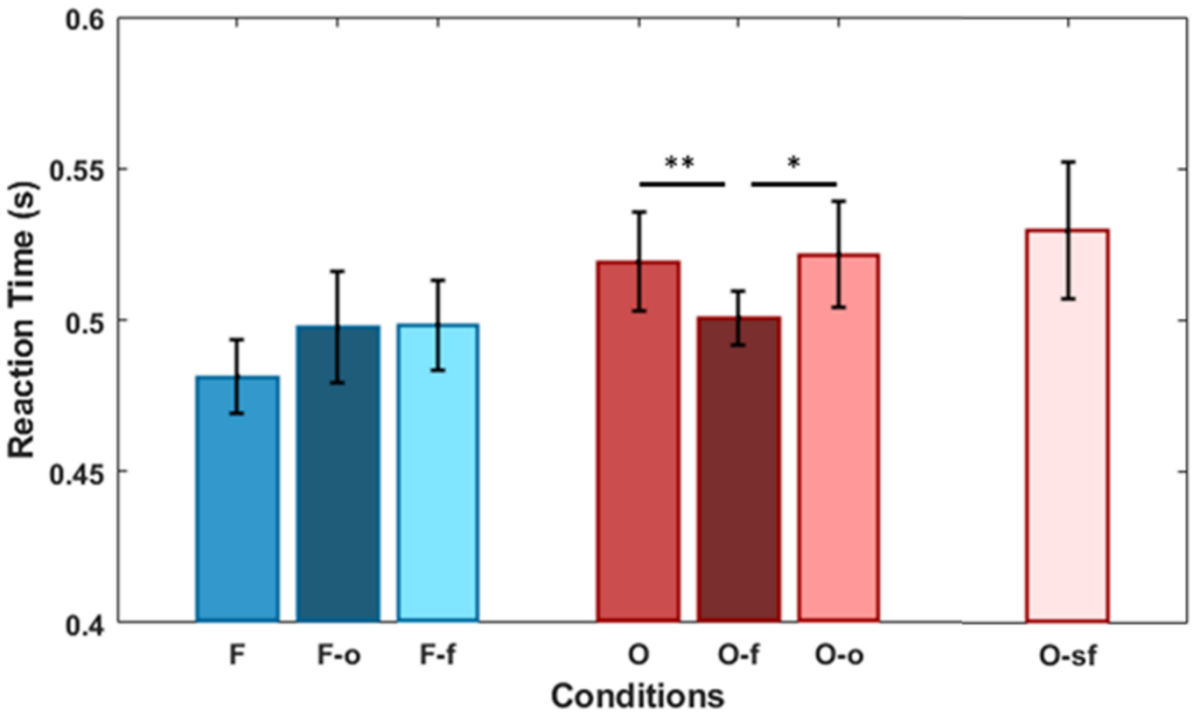

***Figure 3.12**: Results from unilateral and bilateral conditions with real faces stimuli. The upper-case letter indicates the stimulus presented in the intact visual field (F = Familiar, O = Other), whereas lower-case letters, if present, indicates stimuli presented in the blind visual field (f = familiar, o =*

*other, sf = scrambled familiar). Reaction times (seconds ± SD) are based on the performance for the stimulus perceived in the intact field. *p < .05, **p < .01, ***p < .001*

3.4.4 *Discussion*

The main result of this study is that unseen familiar faces presented in the blind field facilitated the processing of stranger faces in a patient affected by Hemianopia and Acquired Prosopagnosia with a wide left-hemisphere lesion affecting occipito-parietal and some portions of the temporal cortices. The patient did not show any summation effects in the RTE, suggesting for the absence of blindsight, neither a significant effect of covert (but conscious) face familiarity processing in the unilateral intact condition, even if it must be noted that a trend for significant difference for cover recognition was found with consistent effect size. In other words, unconscious face-familiarity processing seems to be preserved despite Hemianopia and Acquired Prosopagnosia.

These results are comparable to others found in studies involving RTE in hemianoptic patients with emotional faces (Bertini et al., 2013, 2019; Cecere et al., 2014). In such patients, even in the absence of blindsight-like discrimination skills, the performance in the intact field is enhanced when a fearful face is presented in the blind field, suggesting a crucial contribution of the subcortical pathway that is targeted by emotional stimuli in the absence of the primary cortical visual pathway and visual awareness. Similarly, we found the same results but with a familiar face, and crucially despite Acquired Prosopagnosia. Thus, it is possible that an emotional reaction triggered by the unconscious perception of the familiar face enhanced the processing of the stranger face presented in the intact field – however, to have an emotional reaction assessed by the subcortical pathway, such nuclei must have either processed or received face familiarity information independently from the primary visual pathway and visual awareness.

According to the most influential cognitive model of face perception (Gobbini & Haxby, 2007; Haxby et al., 2000), areas in the core face network such as the occipital face area (OFA) and

the fusiform face area (FFA) in the ventral occipital-temporal cortex process individual and invariant aspects of facial configurations to identify faces (Kanwisher et al., 1997; Yovel & Kanwisher, 2004), and when damaged Acquired Prosopagnosia arises (Barton et al., 2002; Hadjikhani & De Gelder, 2002; Marotta et al., 2001; Rossion, 2008; J. Sergent & Signoret, 1992; Sorger et al., 2007; Steeves et al., 2006). Some argued that deficits in this core face network are mostly related to the apperceptive variant of Prosopagnosia (for a review, see Rivolta et al., 2013). On the other side, the core system forwards information to an extended face network that recruits other cognitive systems to integrate visual face properties with, i.e., memory and emotional features associated with the given face in order to have holistic face perception (Haxby et al., 2000). The two systems communicate through the Inferior Longitudinal Fasciculus connecting occipital and temporal lobes (Catani & Thiebaut de Schotten, 2008; Fox et al., 2008). Within such a model, emotional responses to faces rely on the subcortical structures' activity, which have a pivotal role in processing the emotional significance of stimuli (Tamietto & de Gelder, 2010). Crucially, in the model face recognition is performed by the ventral stream and, only after to recognition, affective responses to faces are provided by limbic structures after FFA inputs (Ellis & Lewis, 2001).

However, there is non-cortico-centric evidence suggesting that subcortical face processing occurs significantly earlier than cortical information processing (for a review, see Johnson, 2005), and other studies suggested that the unconscious face familiarity processing might not depend on structural face processing by cortical activity (Geng et al., 2012; Ota & Nakano, 2021b; Schwartz et al., 2003). The idea behind our results is that it could be possible that the subcortical nuclei can discriminate whether a face is novel or not and assign an emotional reaction with respect to face familiarity independently from cortical processing. Rather than being only influenced by top-down processing from the cortex, subcortical structures also modulate cortical processing – for instance, activity in such pathways predicts the activity of face areas in the cortex (Keightley et al., 2003; Morris, 1998), and FFA showed significant functional connectivity with the amygdala during face

processing of social aspects other than emotional expressions, such as gaze direction (George et al., 2001). Other evidence showed that face-like pattern triggered pulvinar responses before cortical processing (i.e., in around 50ms; Braeutigam et al., 2001; Nguyen et al., 2013, 2014), whereas a study found the amygdala increased responses to neutral faces (Breiter et al., 1996) as compared to scrambled faces (Kesler/West et al., 2001). This is in line with the fact that the behavioral advantage we observed on the intact field disappeared when the scrambled familiar face, rather than the real familiar face, was presented in the blind field. Taken together, these works suggest a broader role of the subcortical pathway triggered by biologically significant facial inputs, subsequently enhancing relevant cortical processing (Johnson, 2005), including face familiarity.

Is it nevertheless possible to exclude a contribution of cortical areas from the effect we found? The answer is probably no. The presence of a subcortical route to the amygdala does not rule out other theoretical explanations or alternative pathways. For instance, both the lateral geniculate nucleus and the pulvinar collaterally project visual information that bypasses V1, targeting extrastriate visual areas in the ventral stream, which can provide feedback to the amygdala (Tamietto & Morrone, 2016). However, even considering that this is a single-case study, the lesion of the patient was not restricted to V1, but consisted in wide portions of occipito-parietal and some temporal areas. As a single brain, we cannot be sure that the areas found through the lesion mapping actually resemble the damaged areas of the patient from a functional point of view (Fox et al., 2009; Saxe, Brett, et al., 2006). This approach revealed that cortical areas of the core face network, such as the Inferior Occipital and the Fusiform Face gyri might be affected by the lesion. This is in line with the neuropsychological evaluation and the patient's report on face *perception*, rather than recognition only, deficits. This suggests for an apperceptive variant of Prosopagnosia, that is indeed thought to be related to damages in the core face network (Rivolta et al., 2013), although we also found consistent damages to the Inferior Longitudinal Fasciculus connecting the core to the extended system of face perception, and such white matter damage is usually attributed to the associative variant of

Prosopagnosia. The Superior Temporal Sulcus (STS), which has an important role in the processing of social stimuli (Lahnakoski et al., 2012) and receiving V1-independent visual inputs from subcortical areas (Sokolov et al., 2012), seems to be spared by the lesion, even if prosopagnosia usually arises after damages in face-specific areas like FFA but not STS (Gainotti & Marra, 2011) as STS has been primarily linked in the representation of dynamic features of faces (Haxby et al., 2000). Thus, given the absence of functional imaging and the limits of single-brain lesion mapping, we can speculate that this alternative hypothesis might be less likely, even if future studies might further investigate such network aspects, and this is possibly the first limit of this study. A second limit relies on the absence of functional or physiological measures to support our results. Sadly, the patient passed out before continuing the next experimental steps involving such follow-ups. Finally, having a control group would have been useful to check for these effects in healthy participants, even if there are studies showing familiarity processing in the absence of awareness and we would not expect any difference in the performance between the patient and healthy controls.

In conclusion, we found that unconscious face familiarity processing is preserved despite Hemianopia and Acquired Prosopagnosia in a patient with left-hemisphere lesions in occipito-parietal cortices and some temporal damages, enhancing the processing of a face stimulus perceived in the intact field. This behavioral facilitation might reflect an early activation of the subcortical pathway for unconscious face perception, assigning an emotional value to the face stimuli. However, to assign emotional values, the brain must discriminate face familiarity. It is plausible that early face processing might simply distinguish whether a face is novel or familiar independently of the geniculo-striatal cortical visual pathway. Instead, it may rely on the preserved subcortical colliculo-pulvinar-amygdala circuit, which might support rapid face-familiarity processing essential for adaptive social behavior. Other works suggested that subcortical mechanisms play a pivotal role in face processing during early development, as cortical structures in newborns are immature (Born et al., 2002; Johnson, 1990; Johnson et al., 1991). This phylogenetically old visual system, known for its role in unconscious

social information processing, may also facilitate early face familiarity recognition, serving as a foundation for the development of the social brain and the cortical face-processing network (Johnson, 2005).

Chapter IV

General Conclusions

'There are many degrees of conscious experience, and the closer science looks, the more blurry the border between conscious and unconscious processing becomes'

Thomas Metzinger, 'The ego Tunnel', 2009

The general aim of this dissertation was to explore the relationship between the bodily-self and visual awareness, exploring how the brain encodes and prioritizes identity-related visual stimuli into conscious perception within two main research lines, respectively focusing on qualitatively different bodily stimuli such as hands and faces. In the first, in three studies we investigated the influence of self-other hand stimuli in the access to visual awareness, testing whereas unconscious perception of bodily effectors might trigger preconscious forms body ownership. In the second, focused on face identity processing, we tested whereas self-face visual stimuli could influence the electrophysiological correlates of visual awareness, and whereas face familiarity processing would still occur in absence of the primary visual pathway necessary for visual awareness in a single patient affected by hemianopia and prosopagnosia.

4.1 *Summary of main findings of Hands Awareness studies*

As for the relation between bodily-self hand stimuli and access to consciousness, *Study 1 & 2* investigated which of the two most important features for bodily self-other distinction, namely the perspective in which they are perceived (i.e., first- vs third-person perspective) and their appearance (i.e., visual details that characterize hand's identity), might affect prioritization in visual awareness. Both perspective and identity-related processing have been shown to have dissociated patterns of

brain activity, for which bodily spatial perspective seems preferentially processed by parietal regions (Astafiev et al., 2004; Carey et al., 2019; Chan et al., 2004; Saxe, Jamal, et al., 2006), and hand's identity by ventral areas of the extrastriate cortex (i.e., EBA; Downing et al., 2001; Myers & Sowden, 2008). *Studies 1 & 2* consistently found a main effect of perspective and absence of identity effects, for which first-person perspective hands were prioritized in the conscious access as compared to third-person perspective despite hand's visual appearance. These results suggest a pivotal role of spatial perspective in attributing hand stimuli to the bodily self before awareness, considering that self-related stimuli are prioritized by the brain (for a review, see Sui & Rotshtein, 2019). It has been claimed that, whereas the ventral stream conveys visual consciousness, unconscious patterns of neural activity might persist in parietal regions along the dorsal stream as also in subcortical nuclei (Fang & He, 2005; Hesselmann, 2013; Hesselmann & Malach, 2011; Ludwig et al., 2015, 2016; Ludwig & Hesselmann, 2015; Milner & Goodale, 2006; Öhman, 2002; Pasley et al., 2004; Zhan et al., 2018). Crucially, the parietal lobe, specifically the left Superior Parietal Lobule (SPL), plays a critical role in representing nearby stimuli within a body-centered coordinate system (Colby & Goldberg, 1999). Notably, these SPL representations are believed to operate predominantly unconsciously (Gray, 2004), as their primary function is to facilitate the visuomotor control of actions. Indeed, a study found that SPL was significantly more activated in first-person perspective as compared to third (Chan et al., 2004). We thus suggested that activity within SPL could represent the neural drive for the faster access to consciousness of first-person perspective hands, as one's own body perception is crucial for correct motor behavior and for interaction with the environment. By contrast, identity-related features seem not to be processed unconsciously as they might represent detailed and redundant information, as we live our entire lives from a first-person perspective that is naturally and predictably attributed to the self.

However, identity played a role in *Study 2*, when a conscious identity prime (i.e., self/other faces) was presented before each bCFS trial to test for effects of top-down contexts on the

unconscious bodily-self attribution of hand stimuli. In fact, self-recognition is a multilevel mechanism in which bottom-up sensory processing and top-down priors and contexts play a role in determining whereas a given object can be categorized as 'mine or not' (for a review, see Apps & Tsakiris, 2014). *Study 2* highlighted that the first-person perspective advantage in the conscious access was significantly reduced with other hands primed with other faces; in other words, in the most ambiguous condition of self-relevance conscious access was slower (Ciorli & Pia, 2024). The predictive processing model for self-recognition argues that an object is attributable to the self if bottom-up sensory prediction and top-down prediction, despite incongruencies between the two, resolve the prediction error in favor of the self. This is in line with the neurocognitive model of body ownership explaining the RHI, in which multisensory conflicts are resolved in favor of vision with the consequent result of embodying a fake rubber hand in one's body schema (Apps & Tsakiris, 2014; Limanowski & Blankenburg, 2016a; Tsakiris, 2010). Thus, it is possible that ambiguous information (other-related) provided by top-down feedback produced a greater prediction error that slowed the conscious access of first-person perspective hands, according to the predictive processing theory applied to conscious perception and the interocular suppression mechanism postulating that visual awareness emerges once prediction errors are minimized (Hohwy et al., 2008; Hohwy & Seth, 2020; Lamme & Roelfsema, 2000).

Unconscious processing of a first-person perspective hands was found not only to boost conscious access, but also to produce embodiment without awareness. That was the research question of *Study 3,* in which we combined CFS and Virtual Reality to test whether body ownership could emerge without the involvement of visual awareness. The preliminary results of this study showed that, when respecting three out of four constraints of body ownership (i.e., the postural, the anatomical, and the peripersonal-space constraints), the embodiment of the virtual hand, as indexed by the proprioceptive drift (i.e., the shift in the perceived position of the real hand toward the fake hand), was induced in absence of visual awareness and despite the multisensory congruency

constrain. Current definitions of body ownership focus on the necessary integration of multimodal congruent stimulations to elicit embodiment over human-like objects (Blanke et al., 2015; Gallagher, 2000; Tsakiris, 2017), even some reported embodiment after just the mere first-person perception (Garbarini et al., 2020; Pyasik et al., 2022). That was replicated only in the conscious version of the VHI paradigm we implemented, whereas the proprioceptive drift was induced despite tactile multisensory congruency in the unconscious condition. Such pattern of results suggests that visuo-tactile congruency might function as a top-down conscious influence to resolve ambiguous information about one's own body. In other words, predictions strongly rooted in perspective might trigger a preconscious form of body ownership integrating first-person hands in the subject peripersonal space unconsciously; such unconscious integration might then be inhibited if conscious processing of multisensory incongruent inputs are provided, or confirmed if congruency is experienced. Surely, perspective has a crucial value in such a process, but another crucial weight for the bodily self is that it is experienced as a multisensory congruent representation (Apps & Tsakiris, 2014; Tsakiris, 2017). However, as previously mentioned, conclusions about this study must be carefully considered given the small sample size we had consequently to the stringent inclusion criteria for the investigation of this phenomenon.

4.2 *Summary of main findings of Face Awareness studies*

Which are the NCCs of visual awareness, also at the electrophysiological level, is still under interesting debate (Dembski et al., 2021; Seth & Bayne, 2022). In *Study 4* we wanted to investigate whether self-face perception might modulate the earliest correlates of visual awareness, the VAN component. Results showed that a greater negative deflection of the VAN component in its peak (i.e., around 250ms) when the self-face was involved, as compared with familiar faces that are associated with both visual exposure and affective components (Gobbini & Haxby, 2007; Ramon & Gobbini, 2018). Moreover, such greater amplitude was observed within the right hemisphere only, the one

which seems more tuned to self-face perception (Janowska et al., 2021; Keenan et al., 2001; Molnar-Szakacs & Uddin, 2023; Uddin et al., 2006). Whereas our study cannot disentangle between perceptual, affective or attentional effects conveyed by the self-face on the VAN, it showed that bodily-self processing is closely linked with visual awareness, which can be affected by high-level stimulus properties in its electrophysiological activity.

Despite *Study 5* not involving the bodily self, it might provide interesting clues on how the brain processes face identity unconsciously. Specifically, we investigated whether face familiarity processing could be preserved in the absence of the primary visual pathway subserving visual consciousness in a single patient affected by hemianopia and acquired prosopagnosia due to extensive left-hemisphere damages including occipito-parietal regions. The results showed that unseen familiar faces presented in the blind field enhanced the processing of stranger faces in the intact field, despite the patient lacking blindsight-like skills or conscious recognition of face familiarity. These findings suggest a preserved subcortical mechanism for unconscious face-familiarity processing, likely mediated by the colliculo-pulvinar-amygdala circuit, given its role in processing biologically significant stimuli (Öhman, 2002; Tamietto & de Gelder, 2010). Within the model of face perception, the core face network (e.g., OFA, FFA) is critical for structural face processing, while the extended network integrates, e.g., emotional and memory-related features (Gobbini & Haxby, 2007; Haxby et al., 2000). It is nevertheless possible that subcortical nuclei, forwarding visual inputs to FFA bypassing V1 (Tamietto & Morrone, 2016), receive identity-related face information and assign emotional values with respect to face familiarity, consequently enhancing the experimental behavioral performance in the intact field (Bertini et al., 2013, 2019; Cecere et al., 2014). However, evidence from this study mostly aligns with non-cortico-centric models, suggesting that subcortical face processing can occur earlier and independently of cortical activity (Johnson, 2005). Indeed, lesion analysis revealed damages to areas linking both the core face network and connections with the extended system, consistently with the apperceptive Prosopagnosia symptoms. It is nevertheless

possible that covert processing in Prosopagnosia rises from preserved subcortical facial emotional processing. These findings possibly provide novel insights into the subcortical pathway's role in face-familiarity processing and its importance for adaptive social behavior, even in the absence of cortical contributions. However, the lack of functional imaging prevents explanatory unanimity on excluding cortical contributions to such effect.

4.3 *General Conclusion*

In conclusion, in five studies this dissertation explored the unconscious self by investigating how the brain encodes bodily visual cues in the absence of awareness, providing evidence that some aspects of the bodily self might not necessitate conscious processing and might directly influence visual awareness. It has been argued that self-consciousness, inherently anchored to the subjective experience, could be built around a hierarchical self-model, with lower-order building blocks of the self largely operating outside the integrated conscious holistic experience (i.e., unconsciously), and a higher-order block of self-processing necessitating consciousness for the highest form of integrated and unified 'aware and alive' experience (Damasio, 1999; Panksepp, 1998; Panksepp & Northoff, 2009). Some hierarchical aspects of the self might be shared across species, whereas others, i.e., the highest form of integrated self-consciousness, might not (see **Fig 4.1**). In this view, consciousness would be specific to the highest form of self-representation, while lower-level forms would operate unconsciously and be characterized by evolutionarily vital functions. For example, in the model postulated by Panksepp and Northoff (2009), the *'proto-self'* (lowest level) operates in forms of processing that are primary and necessary for a bodily sensory processing, while the *'core-self'* is related to a higher (but not highest) self-representation. This core-self, as a mid-level self-representation whose neural basis has been postulated to be in a subcortical-cortical midline, processes implicit, automatic and affective aspects of the self and distinguishes it from the rest of the

environment, as a primary form of self-other distinction. Finally, the highest and most integrated form of the self would be subserved by the cerebral cortex and high-level cognitive functioning.

In this framework, the spatial perspective in which the bodily self is experienced might play a pivotal role in the self-processing of the lower-order core-self, which could trigger unconscious forms of body ownership, despite the crucial role that has been given to multisensory integration for the bodily self-consciousness (Blanke et al., 2015; Gallagher, 2000; Gallup, 1970; Tsakiris, 2017) and information integration for consciousness *per se* (Mashour et al., 2020; Tononi et al., 2016). The congruence of multimodal inputs may be essential for achieving higher-order self-representation, enabling humans and non-human primates to successfully pass the mirror test for self-recognition. However, as all our entire life is experienced in first-person, integrating bodily perspective and forms of self-processing would be highly automatic, predictable, and important for survival, in line with functional mechanisms that characterize unconscious processing, as a building block of the lower-order self-representation that operates outside awareness. Indeed, having an unconscious mechanism that tracks the own body and its movement within the environment, whether it's a human, a tiger, a mouse, is fundamental: and for that form of self-processing, consciousness is very likely to be unnecessary. Then, consciousness might be required to flexibly adjust behavior facing complex contexts and situations (Baars et al., 2013; Cheesman & Merikle, 1986; Dehaene, 2001b; Searle, 1992), as when ambiguous information might challenge such pre-reflective self-construct.

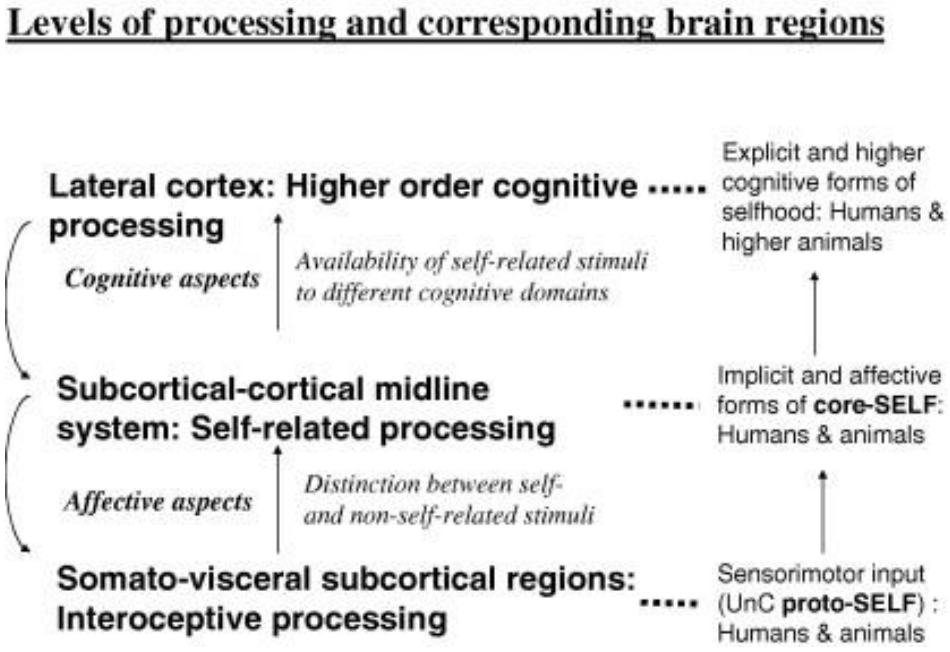

Figure 4.1*: This image was taken from the work by Panksepp and Northoff (2009). It shows a schematic representation of different levels of self that might be shared between animals and humans in relation to possible neural substrates and different aspects of awareness.*

It has been highlighted that a close link between unconscious processing scopes and limits with information processing that is crucial and relevant for survival, often pointing towards phylogenetically older brain areas (i.e., Tamietto & de Gelder, 2010). Even if not unequivocal, it is possible that subcortical nuclei actively participate in social cognition in the absence of awareness, as a key mechanism responding to the relevance of social behavior for humans, as well as parietal areas might subserve unconscious self-other distinction, necessary to have an unconscious representation of the physical substrate of one's existence, a spatial reference for moving in the world we live in as an intrinsically crucial function for survival. An interesting challenge for the future might entail the investigation of neural pathways and functional networks subserving and differentiating the conscious and the unconscious self. Moreover, theories of consciousness might benefit by integrating different aspects of bodily self-consciousness and its neural substrates into their assumptions, as a fundamental aspect of consciousness is its intrinsic connection to the self.

In conclusion, this work suggests that Bodily-Self Consciousness is a highly relevant, automatic, predictable and unconscious process that arises before we even realize being unified and integrated conscious entities.

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