UNIVERSITÀ DEGLI STUDI DI TORINO

DIPARTIMENTO DI PSICOLOGIA

DOTTORATO DI RICERCA IN NEUROSCIENZE

CICLO XXXIV

TITOLO DELLA TESI:

A multisensory account of bodily-self recognition in normal, pathological, and developmental brain

TESI PRESENTATA DA:

Mattia Galigani

TUTOR:

Prof.ssa Francesca Garbarini

COORDINATORE DEL DOTTORATO: Prof. Andrea Calvo

ANNI ACCADEMICI

2018-2022

SETTORE SCIENTIFICO-DISCIPLINARE DI AFFERENZA: M-PSI02

Table of Contents

General introduction

Humans, like other primates, are highly social — indeed, one of our harshest punishments is solitary confinement. Our lives are intertwined with those of other people, and so we must be able to efficiently determine their identities, actions, emotions and intentions. Consequently, a fundamental component of the self is the ability to recognize and represent one's self as distinct from others. The ability to recognize one's own physical features is purportedly possessed by a small selection of primate species, including humans (Anderson & Gallup, 2011; Apps & Tsakiris, 2014; Rochat & Striano, 2000). Since the discovery that chimpanzee are able to pass a simple mirror test (Gallup et al., 1970), there has been a growing and substantial interest in studying self-recognition both in human and non human primates. However, the mechanisms that sustain self-other body discrimination remain, in part, unclear.

The most of information in the field of cognitive neuroscience arises from the intense interest in understanding the neural mechanisms that support face perception (Alzueta et al., 2021; Devue et al., 2007; Sugiura et al., 2015). By contrast, the perception of the rest of the body has until recently received less attention, even though other body parts (i.e., hands) share many characteristics with the face: they convey social information; become highly familiar with repeated exposure over the lifespan; are similar in shape across individuals; and are visually salient, as witnessed by their ability to capture attention. Accordingly, hands also allow us to distinguish our body from others' bodies, as a result of the uniqueness of sensory experience that involve our hands. Indeed, while using our hands, different multisensory signals converge on them, so that we constantly associate visual, tactile and proprioceptive representations of the hands. This hand-related multisensory association may play a crucial role in developing a sense of bodily-self.

As mentioned before, the knowledge of how the brain perceives bodies and how recognizes body identity comes from the study of faces. Importantly, a considerable amount of evidence supports the hypothesis that humans have specialized cognitive and neural mechanisms dedicated to the perception of faces (the face-specificity hypothesis - Kanwisher et al., 1997). Indeed, functional neuroimaging studies have identified a region in the fusiform gyrus, the fusiform face area (FFA), which is activated more strongly by passive viewing of faces compared to objects (Axelrod et al., 2019; Kanwisher et al., 1997; McCarthy et al., 1999). Parallelly, the recordings of electrical and magnetic stimulus-evoked potentials on the scalp show enhanced responses to faces, with peaks at approximately 100 ms, 170 ms, and 250 ms after stimulus onset (De Haan et al., 2002; Jacques & Rossion, 2006; Nasr & Esteky, 2009; Neumann et al., 2011). Most attention has been focused on the negative potential that peaks at posterior sites at about 170 ms (the ‘N170’), which is considered as the electrophysiological marker of face processing. But what for hands? Pioneer works explored the domain of hand recognition and demonstrated that specific brain areas (e.g., the Extrastriate Body Area – EBA) (for a review, see Peelen and Downing, 2007) are involved in the visual processing of hands. Indeed, viewing body representations elicits higher responses in EBA than other stimuli, suggesting a specific role in the visual perception of body parts, including hands (Downing et al., 2001). EBA has also been investigated using transcranial magnetic stimulation (TMS), which provides a complementary approach by producing transient and reversible interference with the activity of the targeted region. Early studies confirmed the implication of EBA in body perception, showing that repetitive TMS (rTMS) over EBA disrupted performance in the visual processing of non-facial body parts (i.e., hands and legs), while leaving unchanged visual processing of face parts and non-corporeal stimuli (Pitcher et al., 2009; Urgesi et al., 2004). Importantly, recent studies also found distinct features of hand processing in the electrophysiological domain, by describing higher N1 amplitude in response to hands than bodies (Espírito Santo et al., 2017) and increased theta power when hands are presented (Moreau et al., 2020).

The described results confirm that our brain is endowed with specific visual areas dedicated to the processing of bodily stimuli. The natural follow up questions concerns the brain mechanisms that allows to discriminate between self and others' bodies. In particular, the key question is whether bodily-self recognition is confined to visual and extrastriate areas or whether other sensory and multisensory areas play a critical role in this process. Several studies point out that distributed brain networks allows to discriminate between the self-face and familiar and unfamiliar faces. Platek et al. (2004) measured BOLD signal response while subjects saw their own face, the face of a stranger, and the face of someone famous. They found that when comparing activation associated with viewing self-faces to viewing famous and novel faces the right hemisphere was selectively active; in particular, self-face recognition preferentially activates the right frontal lobes. Furthermore, Uddin et al. (2005) found activation in right superior frontal and inferior parietal lobes when contrasting self face with varying levels of morphed self faces. They suggest that this activation to "self" represents activation of self–other frontal–parietal mirror network. This idea was also confirmed by Devue et al. (2007) who found activation in anterior (right medial and frontal) regions when distinguishing self face from non-self face. These results suggest that there is a posterior–anterior stream of processing whereby posterior regions serve as first level structural characterization of faces and bodies, whereas anterior regions serve to differentiate self from other at a higher level of processing and perhaps at an abstract level of knowledge about the self.

In the same way, it is reasonable to ask which are the brain processes subserving self-hand recognition. Relevant behavioral evidence point out the existence of different mechanisms support the recognition of self and others' hands (Frassinetti et al., 2010, 2009, 2008). In particular, this series of studies showed a facilitation, in terms of accuracy and response times, when implicitly discriminating pictures representing self-body effectors as compared to others' body effectors (the so-called self-advantage effect). Several works raised the possibility and tested the hypothesis that EBA play a role in processing hand identity. In a TMS study, Urgesi and colleagues (2007) found that the interference with EBA reduces the ability to discriminate between the identity of different hands, thus proving that EBA is causally involved in maintaining an accurate representation of hand shape. Consistent with this, Myers & Sowden (2008) provided evidence that right EBA holds dedicated neural subpopulations that selectively respond to images of our own or others' hands. Their results revealed that neural adaptation differed when presenting sequences containing only others' hands or also the own hand, suggesting that specific neural populations particularly distinguish one's own body parts. However, Chan et al. (2004) tested whether EBA distinguished between egocentric and allocentric views of the self and other bodies. While they also found increased rEBA activity when viewing allocentric relative to egocentric views, identity had no effect in either EBA. In addition, Hodzic et al. (2009) found no modulation of EBA activations in distinguishing self-body from the bodies of familiar others. In the same way, the idea that EBA distinguishes self than other's hand has been also challenged in a TMS experiment relying on the visual enhancement of touch paradigm (vision of the body enhances spatial tactile acuity on the seen body part even if the tactile stimulation is invisible) (Beck et al., 2015). TMS over EBA attenuated the visual enhancement of touch both when participants observed their own hand and another person's hand, suggesting that EBA participates in a common visual representation of the human body with no regard to ownership or identity.

Taken together these results on the role of visual areas in discriminating self than other's hands are controversial. Hence, the natural questions are: What are the brain mechanisms subserving self-hand recognition? Is the visual information only that supports self-hand recognition?

In my thesis, I will describe a series of experiments aimed at investigating how the brain recognize the self hand by using electrophysiological and behavioral techniques in healthy subjects and brain-damaged patients. Specifally, with these studies I will test the hypothesis that self-hand recognition is grounded on the association between visual and sensorimotor representations of the body, rather than on visual features per se. Indeed, differently from others’ bodies, from our hands we constantly receive not only visual information, but also motor, tactile and proprioceptive efferences. In this way, only the visual details that are simultaneously associated with sensorimotor representations (originating from movement perception, position sense, and tactile sensation) can be recognized as belonging to the self-hand and discriminated from the others’ hands.

.

In Chapter 1, I will present a study where we explored visual self-hand recognition by identifying a counterpart of the self-advantage effect with electroencephalography (EEG) (Frassinetti et al., 2008). We took advantage of the mismatch detection phenomenon, which consists of greater electrophysiological responses to a stimulus when it is preceded by a different than an identical one (Ronga et al., 2013; Scannella et al., 2016; Schweinberger & Neumann, 2016; Tugin et al., 2016). Hence, we verified whether, at an electrophysiological level, bodily-self recognition modulates mismatch detection responses. In particular, we recorded event-related potentials while subjects were presented with pairs of visual stimuli that consisted of images of self and others’ hands. If bodily-self recognition actually represents a unique and salient phenomenon, recruiting dedicated mechanisms and neural networks, then we should observe a significant mismatch detection effect only for changing involving images of the self-hand.

Then, capitalizing on the results of the experiment of Chapter 1, we employed a twofold approach (Chapter 2: healthy subjects; Chapter 3: brain-damaged patients) to explore the recruitment of sensorimotor information in self-hand recognition (Ferri et al., 2012; Grivaz et al., 2017; Serino & Haggard, 2010). In Chapter 2, I will address the question of whether the primary somatosensory cortex is involved in the implicit recognition of the self-hand. To this aim, we exploited a recent electrophysiological approach that allows to unveil the contribution of somatosensory areas during a visual task (Arslanova et al., 2019; Galvez-Pol et al., 2020; Sel et al., 2014). This validated method, which entails the subtraction of visual activity from visual-tactile activity. allows examining visually-driven processing of information in cortices other than visual areas, specifically over the somatosensory cortex. In this study, subjects were presented with images depicting self or others' hands and on the half of the trials they also received a concomitant task-irrelevant tactile stimulation to the index fingers of both hands in order to elicit somatosensory evoked activity. If the somatosensory cortex plays a crucial role in bodily-self recognition, we should observe greater somatosensory evoked activity (obtained by subtracting visual from visual-tactile trials) when the self-hand is presented. On the contrary, a comparable somatosensory evoked activity when the self hand and the other's hand are presented would challenge the idea that tactile information is relevant in self-recognition processes.

In Chapter 3, I will explore the contribution of visual-sensorimotor associations in self-hand recognition. To this purpose, we capitalized on brain-damaged patients affected by pathological embodiment. These patients (i.e., E+ patients) misattribute another's persons limb as their own thus suggesting a defective ability in discriminating self and others' body parts (Fossataro et al., 2020; Garbarini et al., 2013, 2014, 2020; Pia et al., 2020; Rossi

Sebastiano et al., 2022). Crucially, the most frequently damaged tract in E+ patients are a fronto-parietal network that is involved in the representation for body action and a posterior occipital network that subserves body form recognition (Errante et al., 2022; Fossataro et al., 2018; Pia et al., 2020). In two behavioral tasks, E+, E- (patients without pathological embodiment) and controls had to implicitly and explicitly recognize the own hand. If spared visual and sensorimotor associations represent the core neural mechanism supporting bodily-self recognition, we anticipated to observe a worst performance in E+ as compared to E- and controls, who both present an intact anterior-occipital connectivity.

In Chapter 4, we moved to a developmental level to prove that establishing visuo-sensorimotor contingencies allows the emergence of bodily-self recognition. To this aim we validated in healthy adults a protocol to identify an implicit marker of self-hand recognition suitable to be applied to newborns and infants. We exploited fast periodic visual stimulation (FPVS) that takes advantage of the consolidated observation that a visual stimulus presented at a given frequency (e.g., 4Hz) elicits an electrical brain activity precisely at the stimulation rates (i.e., 4Hz), measured with electroencephalography (Bottari et al., 2020; Dzhelyova et al., 2017; Rossion et al., 2015, 2020; Zimmermann et al., 2019). This protocol is commonly used to study categorization effects and it is extremely appropriate for developmental studies, because high signal to noise ratio responses can be obtained in few minutes thus complying with the short visual attention of newborns and infants (Buiatti et al., 2019; de Heering & Rossion, 2015). In our pilot study on healthy adults, participants were presented with variable images of strangers' hands at a 4Hz frequency (base stimuli), with images of the self-hand (oddball stimulus) inserted every five images. In a control scenario, we used a constant image of the same stranger's hand as oddball-stimulus. If our protocol in sensitive in highlighting an implicit and reliable marker of self-hand identity recognition, we should observe different oddball responses to self than other's hands.

To summarize, in the present thesis we investigated the mechanisms subserving bodily-self recognition by focusing on the hand, whose multisensory dimension may represent a fundamental mechanisms on which the sense of bodily-self develops. I will start in Experiment 1 by describing an electrophysiological correlate of self-hand recognition and I will proceed by investigating its neural mechanisms in healthy subjects and in brain-damaged patients where the ability to recognize the own hand is lost. Finally, I will describe a validated protocol that lay the basis for future studies to explore the ontogenetic development of self-hand recognition.

References

Alzueta, E., Kessel, D., & Capilla, A. (2021). The upside-down self: One’s own face recognition is affected by inversion. Psychophysiology, July, 1–12. https://doi.org/10.1111/psyp.13919

Anderson, J. R., & Gallup, G. G. (2011). Which primates recognize themselves in mirrors? PLoS Biology, 9(3), 2–4. https://doi.org/10.1371/journal.pbio.1001024

Apps, M. A. J., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. Neuroscience and Biobehavioral Reviews, 41, 85–97. https://doi.org/10.1016/j.neubiorev.2013.01.029

Arslanova, I., Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2019). Searching for bodies: ERP evidence for independent somatosensory processing during visual search for body-related information. NeuroImage, 195(March), 140–149. https://doi.org/10.1016/j.neuroimage.2019.03.037

Axelrod, V., Rozier, C., Malkinson, T. S., Lehongre, K., Adam, C., Lambrecq, V., Navarro, V., & Naccache, L. (2019). Face-selective neurons in the vicinity of the human fusiform face area. Neurology, 92(4), 197–198. https://doi.org/10.1212/WNL.0000000000006806

Beck, B., Bertini, C., Haggard, P., & Làdavas, E. (2015). Dissociable routes for personal and interpersonal visual enhancement of touch. Cortex, 73, 289–297. https://doi.org/10.1016/j.cortex.2015.09.008

Bottari, D., Bednaya, E., Dormal, G., Villwock, A., Dzhelyova, M., Grin, K., Pietrini, P., Ricciardi, E., Rossion, B., & Röder, B. (2020). EEG frequency-tagging demonstrates increased left hemispheric involvement and crossmodal plasticity for face processing in congenitally deaf signers. NeuroImage, 223(August). https://doi.org/10.1016/j.neuroimage.2020.117315

Buiatti, M., Di Giorgio, E., Piazza, M., Polloni, C., Menna, G., Taddei, F., Baldo, E., & Vallortigara, G. (2019). Cortical route for facelike pattern processing in human newborns. Proceedings of the National Academy of Sciences of the United States of America, 116(10), 4625–4630. https://doi.org/10.1073/pnas.1812419116

Chan, A. W. Y., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. NeuroReport, 15(15), 2407–2410. https://doi.org/10.1097/00001756-200410250-00021

De Haan, M., Pascalis, O., & Johnson, M. H. (2002). Specialization of neural mechanisms underlying face recognition in human infants. Journal of Cognitive Neuroscience, 14(2), 199–209. https://doi.org/10.1162/089892902317236849 de Heering, A., & Rossion, B. (2015). Rapid categorization of natural face images in the infant right hemisphere. ELife, 4(JUNE), 1–14. https://doi.org/10.7554/eLife.06564

Devue, C., Collette, F., Balteau, E., Degueldre, C., Luxen, A., Maquet, P., & Brédart, S. (2007). Here I am: The cortical correlates of visual self-recognition. Brain Research, 1143(1), 169–182. https://doi.org/10.1016/j.brainres.2007.01.055

Dzhelyova, M., Jacques, C., & Rossion, B. (2017). At a single glance: Fast periodic visual stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in the human brain. Cerebral Cortex, 27(8), 4106–4123. https://doi.org/10.1093/cercor/bhw223

Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. Science, 293(5539), 2470-2473.

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., & Garbarini, F. (2022). Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Communications, 4(1), 1–15. https://doi.org/10.1093/braincomms/fcac032

Espírito Santo, M. G., Maxim, O. S., & Schürmann, M. (2017). N1 responses to images of hands in occipito-temporal event-related potentials. Neuropsychologia, 106(August), 83–89. https://doi.org/10.1016/j.neuropsychologia.2017.09.012

Fossataro, C., Bruno, V., Bosso, E., Chiotti, V., Gindri, P., Farnè, A., & Garbarini, F. (2020). The sense of body-ownership gates cross-modal improvement of tactile extinction in brain-damaged patients. Cortex, 127, 94–107. https://doi.org/10.1016/j.cortex.2020.02.004

Fossataro, C., Bruno, V., Gindri, P., Pia, L., Berti, A., & Garbarini, F. (2018). Feeling touch on the own hand restores the capacity to visually discriminate it from someone else' hand: Pathological embodiment receding in brain-damaged patients. Cortex, 104, 207–219. https://doi.org/10.1016/j.cortex.2017.06.004

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. Journal of Cognitive Neuroscience, 20(8), 1507–1516. https://doi.org/10.1162/jocn.2008.20067

Gallup, G. G., Anderson, J. R., & Shillito, D. J. (1970). The Mirror Test. The Cognitive Animal, 1–23.

Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2020). Revealing the body in the brain: An ERP method to examine sensorimotor activity during visual perception of body-related information. Cortex, 125, 332–344. https://doi.org/10.1016/j.cortex.2020.01.017

Garbarini, F., Fornia, L., Fossataro, C., Pia, L., Gindri, P., & Berti, A. (2014). Embodiment of others' hands elicits arousal responses similar to one's own hands. Current Biology, 24(16), R738–R739. https://doi.org/10.1016/j.cub.2014.07.023

Garbarini, F., Fossataro, C., Pia, L., & Berti, A. (2020). What pathological embodiment/disembodiment tell us about body representations. Neuropsychologia, 149(October), 107666. https://doi.org/10.1016/j.neuropsychologia.2020.107666

Garbarini, F., Pia, L., Piedimonte, A., Rabuffetti, M., Gindri, P., & Berti, A. (2013). Embodiment of an alien hand interferes with intact-hand movements. Current Biology, 23(2), R57–R58. https://doi.org/10.1016/j.cub.2012.12.003

Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. Human Brain Mapping, 30(3), 951–962. https://doi.org/10.1002/hbm.20558

Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. Psychological Science, 17(6), 485–492. https://doi.org/10.1111/j.1467-9280.2006.01733.x

Kanwisher, N., McDermott, J., & Chun, M. (1997). The Fusiform Face Area: A Module in Human Extrastriate Cortex Specialized for Face Perception. Journal of Neuroscience, 17(11), 4302–4311. https://doi.org/10.1109/CDC.2005.1583375

McCarthy, G., Puce, A., Belger, A., & Allison, T. (1999). Electrophysiological studies of human face perception. II: Response properties of face-specific potentials generated in occipitotemporal cortex. Cerebral Cortex, 9(5), 431–444. https://doi.org/10.1093/cercor/9.5.431

Moreau, Q., Parrotta, E., Era, V., Martelli, M. L., & Candidi, M. (2020). Role of the occipito-temporal theta rhythm in hand visual identification. Journal of Neurophysiology, 123(1), 167–177. https://doi.org/10.1152/jn.00267.2019

Nasr, S., & Esteky, H. (2009). A study of N250 event-related brain potential during face and non-face detection tasks. Journal of Vision, 9(5), 1–14. https://doi.org/10.1167/9.5.5

Neumann, M. F., Mohamed, T. N., & Schweinberger, S. R. (2011). Face and object encoding under perceptual load: ERP evidence. NeuroImage, 54(4), 3021–3027. https://doi.org/10.1016/j.neuroimage.2010.10.075

Pia, L., Fossataro, C., Burin, D., Bruno, V., Spinazzola, L., Gindri, P., Fotopoulou, K., Berti, A., & Garbarini, F. (2020). The anatomo-clinical picture of the pathological embodiment over someone else's body part after stroke. Cortex, 130, 203–219. https://doi.org/10.1016/j.cortex.2020.05.002

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple Dissociation of Faces, Bodies, and Objects in Extrastriate Cortex. Current Biology, 19(4), 319–324. https://doi.org/10.1016/j.cub.2009.01.007

Platek, S. M., Keenan, J. P., Gallup, G. G., & Mohamed, F. B. (2004). Where am I? The neurological correlates of self and other. Cognitive Brain Research, 19(2), 114–122. https://doi.org/10.1016/j.cogbrainres.2003.11.014

Rochat, P., & Striano, T. (2000). Perceived self in infancy. Infant Behavior and Development, 23(3–4), 513–530. https://doi.org/10.1016/S0163-6383(01)00055-8

Ronga, I., Valentini, E., Mouraux, A., & Iannetti, G. D. (2013). Novelty is not enough: Laser-evoked potentials are determined by stimulus saliency, not absolute novelty. Journal of Neurophysiology, 109(3), 692–701. https://doi.org/10.1152/jn.00464.2012

Rossi Sebastiano, A., Poles, K., Miller, L. E., Fossataro, C., Milano, E., Gindri, P., & Garbarini, F. (2022). Reach planning with someone else’s hand. Cortex, 153, 207–219. https://doi.org/10.1016/j.cortex.2022.05.005

Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. European Journal of Neuroscience, 52(10), 4283–4344. https://doi.org/10.1111/ejn.14865

Rossion, B., Torfs, K., Jacques, C., & Liu-Shuang, J. (2015). Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. Journal of Vision, 15(1), 1–18. https://doi.org/10.1167/15.1.18

Scannella, S., Pariente, J., De Boissezon, X., Castel-Lacanal, E., Chauveau, N., Causse, M., Dehais, F., & Pastor, J. (2016). N270 sensitivity to conflict strength and working memory: A combined ERP and sLORETA study. Behavioural Brain Research, 297, 231–240. https://doi.org/10.1016/j.bbr.2015.10.014

Schweinberger, S. R., & Neumann, M. F. (2016). Repetition effects in human ERPs to faces. Cortex, 80, 141–153. https://doi.org/10.1016/j.cortex.2015.11.001

Sel, A., Forster, B., & Calvo-Merino, B. (2014). The emotional homunculus: ERP evidence for independent somatosensory responses during facial emotional processing. Journal of Neuroscience, 34(9), 3263–3267. https://doi.org/10.1523/JNEUROSCI.0106-13.2014

Sugiura, M., Miyauchi, C. M., Kotozaki, Y., Akimoto, Y., Nozawa, T., Yomogida, Y., Hanawa, S., Yamamoto, Y., Sakuma, A., Nakagawa, S., & Kawashima, R. (2015). Neural mechanism for mirrored self-face recognition. Cerebral Cortex, 25(9), 2806–2814. https://doi.org/10.1093/cercor/bhu077

Tugin, S., Hernandez-Pavon, J. C., Ilmoniemi, R. J., & Nikulin, V. V. (2016). Visual deviant stimuli produce mismatch responses in the amplitude dynamics of neuronal oscillations. NeuroImage, 142, 645–655. https://doi.org/10.1016/j.neuroimage.2016.07.024

Uddin, L. Q., Kaplan, J. T., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2005). Self-face recognition activates a frontoparietal “mirror” network in the right hemisphere: An event-related fMRI study. NeuroImage, 25(3), 926–935. https://doi.org/10.1016/j.neuroimage.2004.12.018

Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic Stimulation of Extrastriate Body AreaImpairs Visual Processing of Nonfacial Body Parts. Current Biology, 14, 2130–2134. https://doi.org/DOI 10.1016/j.cub.2004.11.031

Urgesi, C., Candidi, M., Ionta, S., & Aglioti, S. M. (2007). Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. Nature Neuroscience, 10(1), 30–31. https://doi.org/10.1038/nn1815

Zimmermann, F. G. S., Yan, X., & Rossion, B. (2019). An objective, sensitive and ecologically valid neural measure of rapid human individual face recognition. Royal Society Open Science, 6(6). https://doi.org/10.1098/rsos.181904

Chapter 1. Like the back of my hand: Visual ERPs reveal a specific change detection mechanism for the bodily self

[This research has been published in Galigani M, Ronga I, Fossataro C, Bruno V, Castellani N, Rossi Sebastiano A, Forster B, Garbarini F. (2020). Like the back of my hand: Visual ERPs reveal a specific change detection mechanism for the bodily self. Cortex. https://doi.org/10.1016/j.cortex.2020.10.014]

1.1 Introduction

In a series of previous studies employing visual-matching tasks, Frassinetti and colleagues demonstrated that subjects are faster and more accurate in discriminating grey-scale pictures representing bodily-self effectors as compared to others' body effectors (the so-called self-advantage) (Frassinetti et al., 2011; Frassinetti et al., 2008; Frassinetti et al., 2009). The presence of such facilitation in participants' performance has been associated with the recourse to a sensorimotor network recruited when subjects had to recognize the bodily-self in "implicit" tasks (see e.g. Frassinetti et al. 2009; Conson et al., 2017; in other words, the self-recognition is task-irrelevant, i.e. not explicitly required in task instructions).

In the present study, we investigated whether implicit (task-irrelevant), bodily-self recognition has an observable electrophysiological correlate. To this aim, we exploited the mismatch detection phenomenon and we asked whether it could be modulated by implicit, bodily-self recognition. As widely described in the literature, event-related potential (ERP) amplitudes are strongly reduced when the same stimulus is repeated at short and constant time intervals (Iannetti et al., 2008; Wang et al., 2010). Amplitude modulations induced by repetition have also been observed for abstract visual stimuli, such as different shapes (Wang et al., 2004), and body-related pictures, mainly human faces (for a recent review see Schweinberger & Neumann, 2016). Importantly, the detection of a change within stimulus sequence is able to revert such amplitude reduction due to repetition. In other words, the sudden change of one or more stimulus basic features (e.g. modality, intensity, shape, or color) usually enhances the amplitude of the evoked responses (Valentini et al., 2011; Wang et al., 2004). However, this is not always the case. Through a paradigm exploiting intensity modulations of repeated painful stimuli, it has been shown that intensity increases but not decreases could revert repetition-related amplitude reduction (Ronga et al., 2013). The authors interpreted their findings suggesting that only salient changes were able to induce change detection-related responses.

Based on the above evidence (e.g., Frassinetti et al., 2008, 2009), changes involving the self-hand should be considered salient by the nervous system. Previous studies highlighted the specificity of self-hand recognition, which seems to rely on a peculiar sensorimotor mechanism. In other words, the difference between the self- versus other people's hand recognition, by resorting to distinct neural mechanisms, may represent a kind rather than a degree property. It seems therefore likely that stimulus changes involving the self-hand may elicit salience effect (i.e. the reversion of repetition suppression), which are similarly described as kind phenomena. Indeed, as demonstrated by previous studies (Ronga et al., 2013; Torta, Liang, Valentini, Mouraux, & Iannetti, 2012), the change detection effects induced by salient stimuli are expressed in an all or nothing fashion (i.e., the reversion of repetition suppression is not gradable but either present or absent). Analogously, since the self-hand could be more salient than the other's hands, we should expect that only the visual presentation of the self-hand may induce change detection-related responses. Conversely, changes between other people's hands, and even between familiar and not familiar hands, may not be salient enough to revert repetition suppression phenomena.

In our EEG paradigms, ERPs were recorded while participants were presented with grey-scale images depicting the right hands. Hand pictures were delivered in pairs (vS1 and vS2), at a constant 1-second interval, and might represent either the participant's self-hand or other people's hands. Experiment 1 was directed to explore whether the presentation of the self-hand boosts the change detection mechanism, reversing the repetition suppression phenomenon. It was divided into two different conditions (scenarios): in the With Self scenario, the self-hand was included within the presented visual stimuli; in the Without Self scenario, the self-hand was never presented (see 2.1.2 for a rationale description). Subjects were asked to judge whether vS2 was identical or different from vS1 (implicit recognition task). ERPs to visual stimuli, as well as accuracy and response times (RTs) were collected. Experiment 2 specifically aimed at replicating results of Experiment 1 also controlling for any familiarity bias in our behavioral and EEG results. In the design of Experiment 1, the self-hand is the only hand participants had some familiarity with. Therefore, in case we found any specific change detection response for the self-hand, we could not disentangle whether this result was driven by a mechanism specific for the body-self or by a general familiarity effect. To control for this aspect, in Experiment 2 we included a third scenario, namely the With Familiar scenario, where one of the two others' hands was familiar to the participants, by means of repeated presentation of such a hand in the immediately preceding scenario.

From a behavioral point of view, both in Experiments 1 and 2, we expect to confirm the presence of the self-advantage, i.e. higher accuracy and faster RTs any time when at least one self-hand was included in the pair of visual stimuli. From an electrophysiological point of view, if bodily-self recognition actually represents a unique and salient phenomenon, recruiting dedicated mechanisms and neural networks, then in both experiments we should observe a significant change detection effect (i.e. greater amplitude difference between responses to repeated versus non-repeated stimuli) only for images representing the self-hand. Crucially, in Experiment 2 we should observe a clear difference in the change detection responses between the With Self scenario and the With Familiar scenario, with significant change detection effect for the self-hand. We expect that this effect might specifically be observed on the N270 modulation, a component which has been systematically related to visual change detection (Bennett, Duke, & Fuggetta, 2014; Scannella et al., 2016; P. Wang et al., 2018; Zhang et al., 2008). Alternative results, showing a similar change detection effect for self- and other people's hands, would instead challenge the idea of the presence of a specific mechanism for bodily-self recognition.

1.2 Materials and Methods

1.2.1 Experiment 1 (discovery sample)

1.2.1.1 Participants

Fifteen healthy right-handed subjects participated in the study (5 women) aged 22-26 years (mean±SD: 24.1 ±1.2; years of education: 17.9 ±1.0).

Sample size (N=15) was a priori determined to match the number of subjects involved in previous research investigating visual mismatch detection effects and exploiting the same EEG analyses employed in the present study (Wang et al. 2003, N=13; Wang et al. 2004, N=15; Bennet et al. 2014, N=16).

All participants gave their written informed consent to participate in the study, which conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 125055, 12/07/16).

1.2.1.2 Stimuli and Experimental Design

Visual stimuli consisted of grey-scale pictures (10x15 cm) of the dorsum of open right hands belonging either to the participants or to other people. Hand pictures were taken before the experiment, all in the same room, with controlled illumination conditions and were post-processed. As a first step, picture background was removed and replaced with a black uniform background, original color pictures were then converted in grey-scale images with the aim of standardizing different skin colors. Finally, hand images were resized in order to have all similar dimensions. The resulting visual stimuli were presented for 0.3s at the center of a 21-inch Sony CRT computer screen.

The experimental paradigm (presented in Fig. 1) partially replicated the methodology proposed by Frassinetti et al. (2009). However, stimulus presentation parameters (e.g. presentation mode, duration, interstimulus-interval, intertrial-interval) were modified in order to realize a paradigm suitable for EEG. The experiment consisted of a single session divided into two different scenarios (i.e. With Self and Without Self) and four 8-minute recording blocks (2 per scenario). Each scenario was composed of 104 pairs of visual stimuli (vS1 and vS2), delivered at a constant 1 s inter-stimulus interval. The time interval between each pair was randomly jittered between 6 and 8 s, in a way that participants could not anticipate stimulus occurrence.

In both scenarios, vS1 and vS2 could be either identical or different. In the With Self scenario, visual stimuli included participants' self-hand. Four different types of pairs were presented: Self-Self (with both vS1 and vS2 depicting the self-hand); Other1-Other1 (with vS1 and vS2 depicting the same hand belonging to a stranger – Other1); Self-Other1 (with vS1 representing the self-hand and vS2 Other1's hand); Other1-Self (with vS1 representing Other1's hand and vS2 the self-hand).

In the Without Self scenario, the self-hand was never presented. Four different types of pairs were delivered: Other2-Other2 (with vS1 and vS2 depicting the same hand belonging to a stranger – Other2, different from Other1); Other3-Other3 (with both vS1 and vS2 depicting the same hand belonging to a stranger – Other3, different from Other1 and Other2); Other2-Other3 (with vS1 representing Other2's hand and vS2 Other3's hand); Other3-Other2 (with vS1 representing Other3's hand and vS2 Other2's hand). Importantly, in both scenarios the others' hands were matched for the gender of participants. The occurrence of each type of pair (probability of occurrence=0.25) was balanced and pseudo-randomized within each block so that the maximum number of consecutive pairs of the same type was two. Scenarios' presentation order was counterbalanced across subjects (i.e. With Self=A; Without Self=B; one half of the subjects follows the sequence ABBA and the other half BAAB). With the present paradigm, it was possible to compare behavioral and electrophysiological responses to pairs of identical or different visual stimuli, either when the self-hand was present (With Self scenario) or not (Without Self scenario). Crucially, we decided not to intermix all stimulus types (Self, Other1, Other2, Other3) in a single scenario to avoid making self-hand stimuli rare as compared to the other stimuli, always representing strangers' hands.

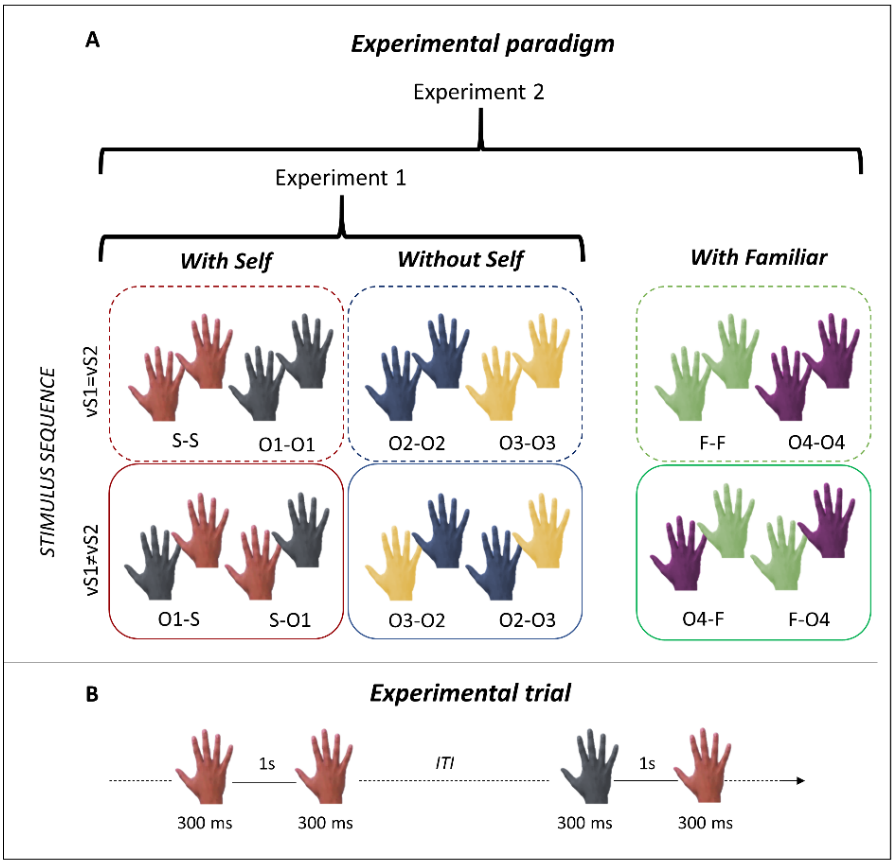


Figure 1 A. Experimental paradigm. Experiment 1 was divided into two different scenarios: With Self (where the self-hand was included), and Without Self (where the self-hand was never presented). Experiment 2 was divided into three different scenarios: With Self, Without Self, and With Familiar (where the familiarized hand was presented). B. Experimental trial. In both experiments, visual stimuli (vS1 and vS2) were displayed for 300 ms and were delivered at a constant 1 s inter-stimulus interval.

1.2.1.3 Behavioral task and EEG recording

During the experiment, participants were seated in a comfortable chair in a silent, dimly lit room, with their chest at a distance of 55 cm from the computer screen. They were asked to focus on the stimuli and look at a fixation cross, placed at the center of the screen. Subjects' task was to decide whether vS2 was identical or different from vS1 by pressing, as fast as possible with the right index finger, the "s" key for identical pairs and the "d" key for different ones on the keyboard. Accuracy and RTs were recorded by Eprime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA).

The EEG was recorded using 32 Ag-AgCl electrodes placed on the scalp according to the International 10-20 system and referenced to the nose. Electrode impedances were kept below 5 kΩ. The electro-oculogram (EOG) was recorded from two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Signals were amplified and digitized at a sampling rate of 1,024 Hz (HandyEEG – SystemPlus Evolution, Micromed, Treviso, Italy).

1.2.1.4 Data Analysis

Behavioral data. Subjects' correct responses (i.e. accuracy) and RTs for each pair type were collected and averaged. Importantly, trials with individual RTs exceeding two standard deviations below or above the mean (of each specific experimental condition) as well as trials with missing or wrong response were discarded from RT analysis (Conson et al., 2015; Ronga et al., 2018; Sarasso et al., 2019). The average number of discarded responses per participant was around 5%. In order to explore the presence of the self-advantage effect in our matching task, we performed, on both accuracy and RTs as dependent variables, separate 2*4 repeated-measures ANOVAs with two within-subject factors: "Scenario" (two levels: With Self scenario; Without Self scenario) and "Condition" (four levels: the two pairs of identical and the two pairs of different stimuli in each scenario). The normal distribution of residuals was checked by using Shapiro-Wilk's test (p always > 0.05). To explore significant interactions, ad hoc planned comparisons were performed and corrected with Bonferroni's test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

Electrophysiological data. ERPs triggered by vS1 and vS2 were pre-processed and analyzed using Letswave v.6 (www.letswave.org) (Mouraux & Iannetti, 2008). Continuous EEG data were segmented into epochs using a time window ranging from 0.5 s before vS1 to 1 s after vS2 (total epoch duration: 3.1 s), and band-pass filtered (1-30 Hz) using a fast Fourier transform filter. Each epoch was baseline corrected using the interval from -0.5 to 0 s as reference. Filter and baseline correction were chosen according to previous studies investigating repetition suppression/change detection paradigms (Galigani et al., under review; Ronga et al., 2013; Torta et al., 2012; Wang et al., 2004; Wang et al., 2003). Artifacts due to eye blinks or eye movements were subtracted using a validated method based on an Independent Component Analysis (ICA – Jung et al. 2000). Finally, epochs belonging to the same pair kind (i.e. 26 epochs) were averaged time-locked to the onset of vS1. Thus, for each subject, eight average waveforms (Self-Self; Other1-Other1; Self-Other1; Other1-Self; Other2-Other2; Other3-Other3; Other2-Other3; Other3-Other2) were obtained.

Statistical analyses on ERPs. The analysis of electrophysiological data was performed on the second stimulus, focusing on the amplitude modulation of the N270 component, which is elicited around 270 ms after stimulus onset, in response to the detection of a mismatch in a pair of visual stimuli (see also § Introduction). Following the same methodology exploited by previous research investigating visual mismatch detection responses (Bennett et al., 2014; Scannella et al., 2016; P. Wang et al., 2018), ERP waveform amplitudes in the time window between 230 and 320 ms after the onset of vS2 were averaged and the resulting value was the object of further analyses. According to previous research (Bennett et al., 2014), mean amplitudes were extracted from four different clusters of electrodes (frontal: F3/Fz/F4; central: C3/Cz/C4; parietal: P3/Pz/P4; occipital: O1/Oz/O2). Importantly, despite the N270 is maximal at fronto-central electrodes (Li et al., 2003; Scannella et al., 2016), we chose to analyse also central, parietal, and occipital clusters in order to have a broad picture of the scalp, as well as to verify that the source of the observed effects matched those described in previous studies. For each cluster, a single mean amplitude value was obtained by averaging each electrode mean amplitude. With the aim of investigating change detection mechanisms for visual stimuli depicting self- versus other people’s hands, the mean amplitudes of N270 extracted from frontal, central, parietal and occipital electrodes were used as dependent variables and entered in four identical statistical models (one for each cluster), i.e. a 2*4 repeated measures ANOVA with two within-subject factors: “Stimulus Sequence” (two levels: vS1=vS2, vS1≠vS2); and “Stimulus Identity” of vS2 (four levels: Self, Other1, Other2, Other3). The normal distribution of residuals was checked by using Shapiro-Wilk‘s test (p always > 0.06). Post hoc comparisons were performed by means of Bonferroni’s test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

1.2.2 Experiment 2 (replicating sample and control for familiarity bias)

1.2.2.1 Participants

Fifteen healthy right-handed subjects participated in the study (10 women) aged 19-30 years (mean±SD: 24.88±3.1; years of education: 18.1±2.7). None of them participated to Experiment 1. Sample size (N=15) was a priori determined to match the sample of Experiment 1. All participants gave their written informed consent to participate in the study, which conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 125055, 12/07/16).

1.2.2.2 Stimuli and Experimental Design

General procedures were identical to the Experiment 1, with the following exceptions. In the experimental paradigm (Fig. 1) we included a third scenario, i.e. the With Familiar scenario. In this scenario, we presented two others' hands. Importantly, one of these hands was familiar for the participant (i.e. the Familiar hand), since it had already been repeatedly presented in the immediately preceding scenario (which, depending on the specific sequence assigned to subject, might either be the With Self or the Without Self scenario). Four different pair types were presented: Familiar-Familiar (with both vS1 and vS2 depicting the familiarized hand); Other4-Other4 (with vS1 and vS2 depicting the same hand belonging to a stranger – Other4); Familiar-Other4 (with vS1 representing the familiarized hand and vS2 Other4's hand); Other4-Familiar (with vS1 representing Other4's hand and vS2 the familiarized hand). The occurrence of each pair type (p=.25) was matched across conditions and pseudo-randomized within each block, so that the maximum number of consecutive pairs of the same type was two. The presentation of the scenarios was counterbalanced, except for the With Familiar scenario that was always presented immediately following the scenario including the other's hand with which participants familiarized (i.e. With Self=A; Without Self=B; With Familiar=C; subjects may be administered with one of the following sequences: ACB; BAC; BCA; ABC).

Furthermore, in order to exclude that any possible negative results observed in Experiment 1 (such as the absence of a significant change detection effect in the Without Self scenario) were due to a signal to noise ratio problem rather than to a genuine absence of modulation, we doubled the number of trials in Experiment 2 (i.e. 52 trials per condition). Each scenario was therefore composed of 208 pairs of visual stimuli (vS1 and vS2), delivered at a constant 1 s inter-stimulus interval. The time interval between each pair was randomly jittered between 3 and 4 s, in a way that participants could not anticipate stimulus occurrence. The whole experiment was divided into six 8-minute recording blocks (2 per scenario).

1.2.2.3 Behavioral task and EEG recording

All procedures were identical to those of Experiment 1.

1.2.2.4 Data Analysis

Behavioral data. Subjects' correct responses (i.e. accuracy) and RTs for each pair type were collected and averaged. Importantly, trials with individual RTs exceeding two standard deviations below or above the mean (of each specific experimental condition) as well as trials with missing or wrong response were discarded (Bruno et al., 2019; Bruno et al., 2020; Conson et al., 2015; Fossataro, Bucchioni, et al., 2018; Ronga et al., 2018; Sarasso et al., 2018). The average number of discarded responses per participant was around 5%. In order to explore the presence of the self-advantage effect in our matching task, we performed, on both accuracy and RTs as dependent variables, two 3*4 repeated-measures ANOVA with two within-subject factors: "Scenario" (three levels: With Self scenario; Without Self scenario; With Familiar scenario) and "Condition" (four levels: the two pairs of identical and the two pairs of different stimuli in each scenario). The normal distribution of residuals was checked by using Shapiro-Wilk's test (p always > 0.05). To explore significant interactions, ad hoc planned comparisons were performed and corrected with Bonferroni's test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

Electrophysiological data. All the preprocessing of ERP data was identical to that of Experiment 1, except for the following. We obtained 52 epochs for each pair that were averaged time-locked to the onset of vS1. Thus, for each subject, twelve average waveforms (Self-Self;

Other-Other; Self-Other; Other-Self; Other1-Other1; Other2-Other2; Other2-Other1; Other1-Other2; Familiar-Other3; Other3-Other3; Ohter3-Familiar; Familiar-Other3) were obtained. The normal distribution of residuals was checked by using Shapiro-Wilk‘s test (p always > 0.06). Post hoc comparisons were performed by means of Bonferroni’s test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

Statistical analyses on ERPs. The analysis of electrophysiological data replicated that of Experiment 1. The mean amplitudes of N270 extracted from frontal, central, parietal and occipital clusters were used as dependent variables and entered in four identical statistical models (one for each cluster), i.e. 2x6 repeated measures ANOVAs with two within-subject factors: “Stimulus Sequence” (two levels: vS1=vS2, vS1≠vS2); and “Stimulus Identity” of vS2 (six levels: Self, Other1, Other2, Other3, Other4, Familiar). The normal distribution of residuals was checked by using Shapiro-Wilk‘s test (p always > 0.07). Post hoc comparisons were performed by means of Bonferroni’s test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

1.3 Results

1.3.1 Experiment 1 (discovering sample)

1.3.1.1 Behavioral results

Behavioral results are presented in Figure 2. Note that, overall are in line with our predictions, participants showed a more accurate and faster behavioral performance anytime the self-hand was included in the pair, thus indicating the presence of the self-advantage effect also in our sample.

Accuracy

The 2*4 repeated measures ANOVA performed on accuracy values revealed a significant Scenario*Condition Interaction ($F_{3,42}=4.967$; $p=0.004$; $\eta 2=0.262$), showing that the factor Condition was significantly modulated only in the With Self scenario. To further explore this interaction, four planned comparisons were run in the With Self scenario to compare identical pairs (Self-Self vs Other1-Other1), different pairs (Other1-Self and Self-Other1) and each identical pair with the corresponding different pair (Self-Self vs Other1-Self; Other1-Other1 vs Self-Other1). By applying Bonferroni's correction, alpha value was set at 0.012. Crucially, planned comparisons revealed that accuracy values of the Self-Self pair (mean±SEM= 93.71±2.09 %) were higher, even though it did not reach the significance level after Bonferroni's correction ($p=0.012$), than those of Other1-Other1 pair (mean±SEM= 83.64±3.81 %), whereas the accuracy rate of Other1-Self pair (mean±SEM= 94.59±1.71 %) and Self-Other1 pair (mean±SEM=89.64±2.79 %) were not significantly different ($p=0.048$). Moreover, the percentage of accuracy response were higher in Self-Other1 pair as compared to Other1-Other1 pair, even though the difference did not reach the significance level ($p=0.014$), but no significant differences emerged comparing Self-Self pairs to Other1-Self pair ($p=0.683$). This suggests the presence of a higher accuracy anytime the self-hand was included in the pair.

Response Times (RTs)

The 2*4 repeated measures ANOVA performed on RTs revealed a significant Scenario*Condition Interaction ($F_{3,42}=3.820$; $p=0.016$; $\eta 2=0.214$). Crucially, as for the accuracy, the factor Condition was modulated only in the With Self scenario and it was further explored with four planned comparisons (see above). Faster RTs were found in Self-Self pair (mean±SEM= 675.42±52.50 ms) as compared to Other1-Other1 pair (mean±SEM= 745.72±49.25 ms), even though the difference did not reach the significance level ($p=0.017$), whereas RTs of Other1-Self pair (mean±SEM= 727.64± 56.2 ms) and Self-Other1 pair (mean±SEM= 680.16±52.78 ms) were not significantly different ($p=0.057$). Moreover, behavioral performance was significantly faster in Self-Other1 pair as compared to Other1-Other1 pair (p=0.0119), but no significant differences emerged comparing Self-Self pair to Other1-Self pair (p=0.102). Overall, the RT results parallel the accuracy results, showing the presence of a faster response anytime the self-hand was included in the pair.

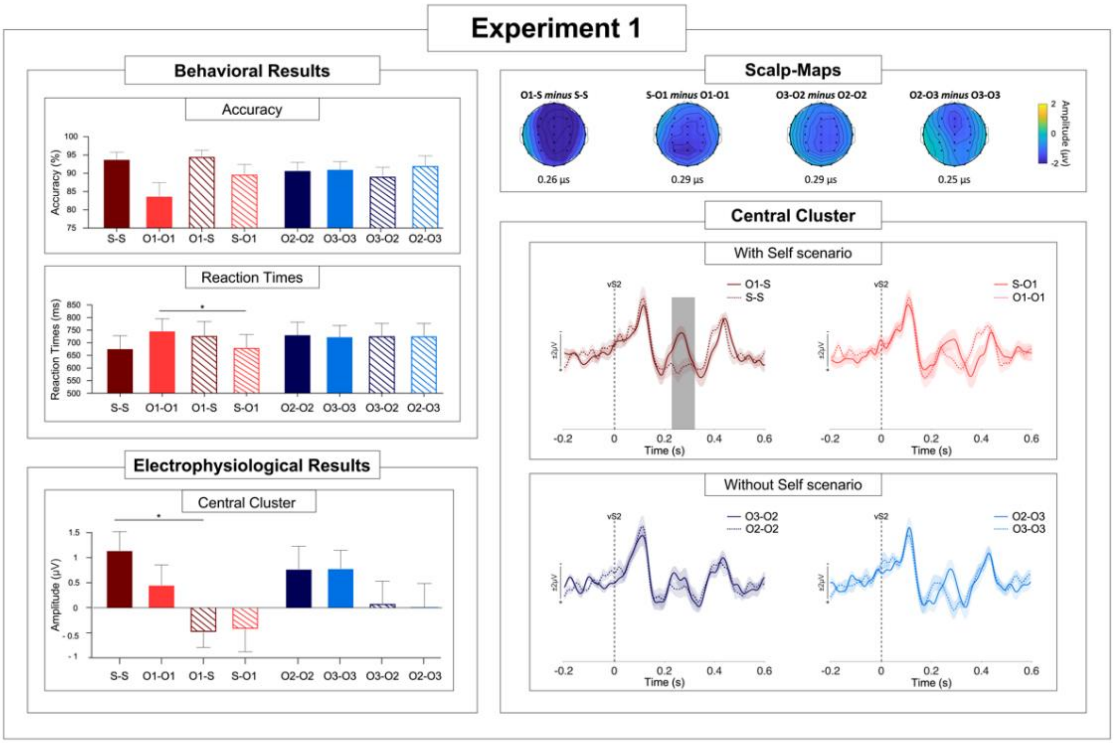


Figure 2. Experiment 1: behavioral and electrophysiological results. The top left panel represents the accuracy values (in percentages) and the subjects' RTs. Note that subjects' performance was more accurate and faster anytime the self-hand was presented. The bottom left panel represents the mean of ERP amplitudes in the range between 230 and 320 ms post vS2 onset (i.e. the window including N270 component). Y axis: the mean voltage amplitude (µV); X axis: experimental conditions. Note that the With Self scenario is represented in red, while the Without Self scenario is represented in blue. The top right panel represents the scalp map distribution of change response peaks (the latency corresponds to the peak of the subtractions waves). Maps are obtained by subtracting the response to vS2 of identical pairs from the response of vS2 of different pairs. The bottom right panel represents ERP waveforms in response to the vS2 at the central cluster (mean of the electrodes composing the cluster). Y axis:

amplitude (μV); X Axis: time (s). Waveforms in dotted lines represent pairs of identical stimuli (vS1=vS2), waveforms in solid lines represent pairs of different stimuli (vS1□vS2). Shaded areas correspond to ERP sem (standard error of the mean). Significant differences are highlighted in grey. The top panel represents ERP waveforms in the With Self scenario. The bottom panel represents ERP waveforms in the Without Self scenario.

1.3.1.2 ERP results

Electrophysiological results for the central cluster are presented in Figure 2.

Note that, as expected, the contrast between pairs of identical stimuli (vS1=vS2) and pairs of different stimuli (vS1≠vS2) revealed a greater differential amplitude of the N270 in the With Self scenario when vS2 represented the self-hand (i.e. Self-Self vs. Other1-Self).

Frontal cluster

The 2*4 repeated measures ANOVA revealed a main effect of Sequence (F1,14= 6.949; p=0.019; η2=0.331), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= 0.16±0.29 μV; vS1≠vS2: mean±SEM= -0.60±0.33 μV). A significant Sequence*Identity interaction (F3,42= 2.974; p=0.042; η2=0.175) was observed, suggesting that the difference between identical and different pairs was greater when vS2 represented the self-hand. Crucially, post-hoc analyses showed that only the Self-Self vs Other1-Self comparison was significantly different in the N270 time window, with a larger amplitude for the different as compared to the identical pair (p<0.001). All other comparisons were ≥0.60.

Central cluster

The 2*4 repeated measures ANOVA revealed a main effect of Sequence (F1,14= 13.926; p=0.002; η2=0.499), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= 0.76±0.34 μV; vS1≠vS2: mean±SEM= -0.18±0.35 μV). A significant Sequence*Identity interaction (F3,42= 3,067; p=0.038; η2=0.180) was found. As for the frontal cluster, post-hoc comparisons showed that only Self-Self vs Other1-Self was significant, with a larger amplitude for the different as compared to the identical pair (p<0.001). All other comparisons were ≥0.08.

Parietal cluster

The 2*4 repeated measures ANOVA revealed a main effect of Sequence (F1,14= 14.705; p=0.002; η2=0.512), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= 1.27±0.32 μV; vS1≠vS2: mean±SEM= 0.51±0.29 μV). Moreover, no significant Sequence*Identity interaction was found (F3,42= 2,822; p=0.051; η2=0.168).

Occipital cluster

The 2*4 repeated measures ANOVA revealed a main effect of Sequence (F1,14= 5.106; p=0.040; η2=0.267), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= 1.60±1.56 μV; vS1≠vS2: mean±SEM= 1.05±0.38 μV). Moreover, no significant Sequence*Identity interaction was found (F3,42= 2.686; p=0.059; η2=0.161).

1.3.2 Experiment 2 (replicating sample and control for familiarity)

1.3.2.1 Behavioral results

Behavioral results are presented in Figure 3. Note that behavioral results replicate the results of Experiment 1, showing a more accurate and faster performance anytime the self-hand was presented.

<u>Accuracy</u>

The 3*4 repeated measures ANOVA performed on accuracy values revealed a significant Scenario*Condition Interaction (F6,84=5.130; p<0.001; η2=0.268), showing that the factor Condition was modulated only in the With Self scenario. As for the Experiment 1, to further explore this interaction, four planned comparisons were run in the With Self scenario to compare identical pairs (Self-Self vs Other1-Other1), different pairs (Other1-Self and Self-Other1) and each identical pair with the corresponding different pair (Self-Self vs Other1-Self; Other1-Other1 vs Self-Other1)-. By applying Bonferroni's correction, alpha value was set at 0.012. Planned comparisons revealed that accuracy values of the Self-Self pair (mean±SEM= 96.60±1.04 %) were significantly higher (p<0.001) than those of Other1-Other1 pair (mean±SEM= 85.57±2.18 %), whereas the accuracy rate of Other1-Self pair (mean±SEM= 89.46±2.36 %) and Self-Other1 pair (mean±SEM=92.09±2.34 %) were not significantly different (p=0.266). Moreover, the percentage of accuracy response were significantly higher in Self-Other1 pair as compared to Other1-Other1 pair (p<0.001) and in Self-Self pair as compared to Other1-Self pair, even if it did not reach the significance level (p=0.012), suggesting that the greater the accuracy the greater the presence of self-hand in the pair.

<u>Response Times (RTs)</u>

The 3*4 repeated measures ANOVA performed on accuracy values revealed a significant Scenario*Condition interaction ($F_{6,84}=5.555$; $p<0.001$; $\eta 2=0.284$), showing that, as for the accuracy, the factor Condition was modulated only in the With Self scenario. All planned comparisons performed in the With Self scenario were significant here, revealing that RTs of the Self-Self pair (mean±SEM= 623.81±48.34 ms) were significantly faster ($p=0.003$) than those of Other1-Other1 pair (mean±SEM= 732.31±39.78 ms) and that RTs in Self-Other1 pair (mean±SEM= 642.16±46.37 ms) were significantly faster ($p<0.001$) as compared to Other1-Self pair (mean± SEM=702.1742.74 ms). Moreover, RTs were significantly faster in Self-Other1 pair as compared to Other1-Other1 pair ($p<0,001$) and in Self-Self pair as compared to Other1-Self pair ($p=0.010$), suggesting that the behavioral performance was faster whenever the self-hand was present in the pair and it was depicted as the first stimulus.

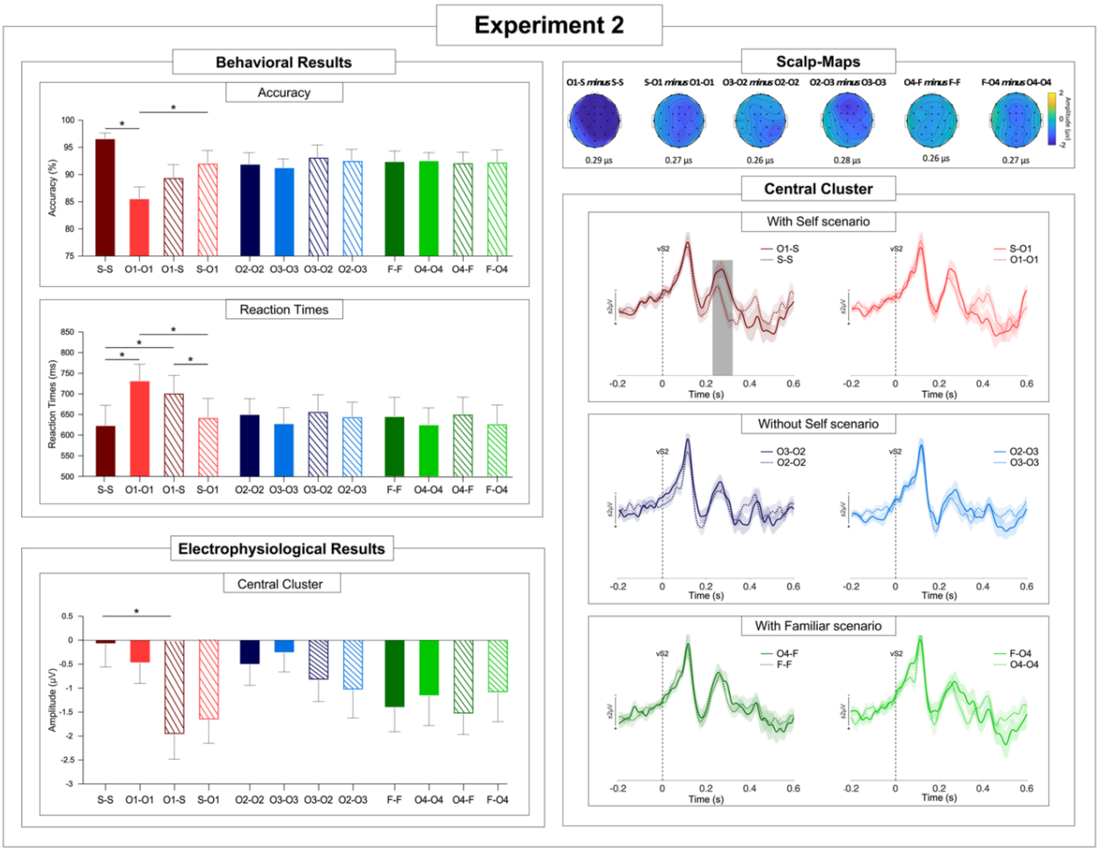


Figure 3. Experiment 2: behavioral and electrophysiological results. The top left panel represents the accuracy values (in percentages) and the subjects' RTs. Note that subjects' performance was more

accurate and faster anytime the self-hand was presented. The bottom left panel represents the mean of ERP amplitudes in the range between 230 and 320 ms post vS2 onset (i.e. the window including N270 component). Y axis: the mean voltage amplitude (µV); X axis: experimental conditions. Note that the With Self scenario is represented in red, while the Without Self scenario is represented in blue, and the With Familiar scenario in green. The top right panel represents the scalp map distribution of change response peaks (the latency corresponds to the peak of the subtractions waves). Maps are obtained by subtracting the response to vS2 of identical pairs from the response of vS2 of different pairs. The bottom right panel represents ERP waveforms in response to the vS2 at the central cluster (mean of the electrodes composing the cluster). Y axis: amplitude (µV); X Axis: time (s). Waveforms in dotted lines represent pairs of identical stimuli (vS1=vS2), waveforms in solid lines represent pairs of different stimuli (vS1≠vS2). Shaded areas correspond to ERP sem (standard error of the mean). Significant differences are highlighted in grey. The top panel represents ERP waveforms in the With Self scenario. The middle panel represents ERP waveforms in the Without Self scenario. The bottom panel represents ERP waveforms in the With Familiar scenario.

Notably, overall present results confirmed the findings of Experiment 1.

1.3.2.2 ERP results

Electrophysiological results for the central cluster are presented in Figure 3. Results for all the other clusters are presented in the Supplementary materials.

Note that, as in Experiment 1, the contrast between pairs of identical (vS1=vS2) and different stimuli (vS1≠vS2) revealed a significant modulation of the N270 only in the Whit Self scenario when vS2 represented the self-hand.

Frontal cluster

The 2*6 repeated measures ANOVA revealed a main effect of Sequence (F1,14=15,013; p=0.002; η2=0.517), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= -0.54±0.25 μV; vS1≠vS2: mean±SEM= -1.35±0.29 μV). A significant Sequence*Identity interaction was found (F5,70= 4.895; p<0.001; η2=0.259). Crucially, post-hoc comparisons showed that only vS2s belonging to Self-Self vs Other1-Self pairs were significantly different in the N270 time window, with a significantly larger amplitude for the different as compared to the identical pair (p<0.001). All other comparisons were ≥0.08.

Central cluster

The 2*6 repeated measures ANOVA revealed a main effect of Sequence (F1,14=12.186; p=0.004; η2=0.465), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= -0.38±0.34 μV; vS1≠vS2: mean±SEM= -1.15±0.39 μV). A significant Sequence*Identity interaction was found (F5,70= 3.621; p=0.006; η2=0.201). Crucially, post-hoc comparisons showed that only S2s belonging to Self-Self vs Other1-Self pairs were significantly different in the N270 time window, with a significantly larger amplitude for the different as compared to the identical pair (p<0.001). All other comparisons were ≥0.71.

Parietal cluster

The 2*6 repeated measures ANOVA revealed a main effect of Sequence (F1,14=11.462; p=.004; η2=0.450), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= 0.26±0.36 μV; vS1≠vS2: mean±SEM= -0.38±0.43 μV).). No significant Sequence*Identity interaction was found (F5,70= 2.154; p=0.069; η2=0.133).

Occipital cluster

The 2*6 repeated measures ANOVA revealed a main effect of Sequence ($F_{1,14}=9.257$; $p=0.009$; $\eta^2=0.398$), with overall larger ERP amplitudes for different as compared to identical vS2 (vS1=vS2: mean±SEM= -0.07±0.51 μV; vS1≠vS2: mean±SEM= -0.66±0.63 μV). No significant Sequence*Identity interaction was found ($F_{5,70}= 0.677$; $p=0.642$; $\eta^2=0.046$).

1.4 Discussion

The present paper, focused on bodily self-identification, explores whether the recognition of our physical identity has an observable electrophysiological correlate. More specifically, we exploited the amplitude modulation following different vs identical stimulation to verify whether implicit bodily-self recognition is able to modulate change detection responses, in a pair of sequentially presented visual stimuli. Importantly, previous literature investigating body-related change detection within the visual domain has mainly concentrated on face discrimination (Schweinberger & Neumann, 2016). Crucially, face visual features are extremely salient, since they are systematically employed for individual recognition. Still, self-face recognition seems to rely on sensorimotor representations, exploiting multisensory cues, such as speech processing (Cardini et al., 2011; Sugiura, 2015; Tsakiris, 2008). Not surprisingly, therefore, face changes induced change detection responses in visual evoked potentials. Conversely, the present study focuses on body effectors (right hands), whose visual features are not equally relevant for their discrimination. However, similarly to faces, the self-hand representation is supposed to recruit not only visual, but also sensorimotor brain networks (Apps & Tsakiris, 2014; Conson et al., 2017; Ferri et al., 2012; Limanowski & Blankenburg, 2015). Thus, thanks to this multimodal representation, we hypothesized that self-hand visual recognition should still entail a special change detection mechanism, inducing greater electrophysiological responses than those elicited by others' hands discrimination.

In the following paragraphs we (1) outline our behavioral findings as supporting evidence of the self-advantage effect and (2) discuss our ERPs results, which seem to confirm the salience of bodily-self stimuli, which are able to boost identity recognition and change detection both at behavioral and at electrophysiological levels. Importantly, the results highlighted in Experiment 1 (our discovering sample) were fully confirmed and extended in Experiment 2, which, besides controlling for a possible familiarity bias in our change detection effect, can be considered as a measure of internal replicability.

The self-advantage and visual ERPs

Our behavioral results highlighted the relevance of self-advantage (Frassinetti et al., 2009) in a repetition suppression paradigm, thus confirming the presence of such an effect for detection tasks, even though self-recognition is not explicitly required by experimental instructions.

In both experiments, participants' accuracy rate was modulated selectively in the With Self scenario (as indicated by the significant interaction between the factors Sequence and Identity in Experiments 1 and 2 - § Results 3.1.1; 3.2.1), where participants' performance was overall more accurate whenever the self-hand was included in the pair. The statistical analyses on RTs paralleled accuracy results, thus reveling a significant modulation only in the With Self scenario. In both experiments, we observed a comparable pattern of results, showing a complete replicability of our findings. Interestingly, in the RT analysis of Experiment 2, likely because of the increased number of trials included in this second experiment, all the planned comparisons were significant, thus showing RT facilitation anytime the self-hand was the first stimulus of the pair. To explain this result, we can hypothesize that the self-hand, when presented as the first stimulus, boosted subjects' working memory and thanks to its relevance for the system reduced the cognitive load and facilitated the active maintenance of the stimulus memory trace in order to solve the task (Scannella et al., 2016).

Taken together, both accuracy and RTs point out a clear self-advantage effect in our behavioral results, with overall faster and better performance when the self-hand was included in the pair.

From an electrophysiological point of view, as indicated by previous literature (Iannetti et al., 2008; Ronga et al., 2013), we hypothesized a significantly different ERP amplitude modulation between repeated and non-repeated conditions, highlighting, at least in the With Self scenario, a specific change detection mechanism. The present ERP data confirm our hypothesis (see below). Still, electrophysiological results in a way paralleled our behavioral findings, since in both experiments all significant modulations were selectively observed in the With Self scenario, thus pointing out the relevance of bodily-self recognition both from a behavioral and an electrophysiological point of view.

The specific change detection mechanism for self-the hand is revealed by N270 amplitude modulation From an electrophysiological point of view, in both experiments, we found a main effect of Stimulus Sequence, thus confirming also in the present samples the sensitivity of N270 component in revealing sudden mismatches in a stream of visual stimuli (Wang et al., 2004; Wang et al., 2003). Ferrari, Bradley, Codispoti, and Lang (2010), by employing an oddball task with picture sequences, showed that N270 amplitude dramatically decreased already after the first stimulus repetition and immediately increased for novel pictures, thus confirming results by Wang et al. (2004) obtained with stimulus pairs. Furthermore, the presence of overall greater N270 amplitudes when vS2 was different rather than identical to vS1, is in line with earlier evidence, proposing the N270 as an electrophysiological biomarker of conflict detection in a sequence of incoming visual stimuli (Enriquez-Geppert et al., 2010; Folstein & Van Petten, 2008).

More crucially for the present study, we also found a significant interaction between the factors Sequence and Identity, thus indicating that N270 amplitude was selectively modulated in the With Self scenario. Post-hoc comparisons revealed that the amplitude modulation between identical vs different pairs (i.e. change detection) was significant only for stimuli representing the self-hand. Notably, this effect was found mainly over frontal and central electrodes, where in both experiments it was fully significant. For the parietal and occipital clusters, we found no significant modulations in both Experiment 1 and 2. These results are fully consistent with source localization studies, showing a fronto-central distribution of the N270 component (Li et al., 2003; Scannella et al., 2016).

The confinement of significant change detection effects to the With Self scenario is a crucial finding since, as expected, it demonstrates that a reversion of repetition suppression mechanism within the N270 time window are not automatically elicited by the system anytime a change in the stimulation pattern occurs. Instead, mismatch detection responses emerge only when stimulation changes are valued as salient (Ronga et al., 2013). Importantly, our results confirm that the salience of the self-hand, as demonstrated by its ability to revert repetition suppression effectively, represents a kind rather than a degree property expressed by all or nothing effects. Interestingly, such salience of self-recognition turns up even when entailing the (task-irrelevant) identification of body effectors, selectively through their visual appearances. Apparently, recognizing our own body seems to represent an aprioristic relevant matter for the individual, independently from specific task instructions.

A similar line of research, focused on investigating the electrophysiological signatures of self and other's face recognition, reported that the amplitude of an occipito-temporal negative component, peaking around 250 ms post stimulus onset, appeared larger in response to familiar, rather than unfamiliar faces (Schweinberger & Neumann, 2016; Tanaka & Pierce, 2009). Even though such a component was emerging from different neural sources as compared to our fronto-central N270 (see e.g., Caharel al., 2009), results of Experiment 1 cannot exclude that the familiarity of the self-hand could somehow contribute to N270 modulation in the With Self scenario. To explore this possible familiarity-related effect and confirm the results of Experiment 1, we run Experiment 2, where a scenario with a familiar hand was added in the experimental paradigm. Importantly, and as supporting evidence of the specificity of our effect for the self-hand, we found that presenting a familiarized hand did not boost change detection responses (as demonstrated by the absence of any behavioral and electrophysiological modulations in the With Familiar scenario – see 3.2.1 and 3.2.2). This finding seems to indicate that the enhancement of change detection mechanisms is driven by a self-specific effect and not by a mere familiarity effect, even though we cannot rule out that the special familiarity acquired by the self-hand somehow contributed to the observed effect.

Overall, it may be challenging to distinguish specific self-recognition driven effects from familiarity-driven effects and previous studies present controversial evidence. Butler and colleagues (Butler al., 2013) found similar electrophysiological signatures of self-face and highly familiar faces (i.e., those of dizygotic twins), suggesting that self-bodies, when compared to other bodies with a similar exposure, do not involve unique featural encoding. On the other hand, Alzueta et al. (2019) recorded EEG activity while participants performed a facial recognition task, where they had to discriminate between their own face, a friend's face, and an unknown face. Crucially, authors pinpointed a specific modulation (within the time window of P200), distinctive of the processing of self-face, suggesting that self-body parts have dedicated processing mechanisms, clearly distinguishable from the detection of others' familiar bodies. We believe that our results, revealing a selective modulation of N270 component only when the self-hand was presented, may be considered as a supporting evidence of the tenet that self and other body parts have different neural representations (see below).

Overall the present findings suggest that, in a visual detection task, self- and only self-hand changes are salient enough to reverse repetition suppression mechanism. In other words, self-hand recognition, similarly to other sensory stimulation valued as relevant by the system, might trigger the activity of the "salience network" (mainly including multimodal, associative cortices, such as the anterior cingulate cortex and the insula) (Legrain al., 2011; Mouraux al., 2011), thus boosting the mismatch detection effect. However, this possible mechanism does not explain how the system recognizes the self-hand. Previous studies showed that the nervous system may employ a number of different strategies to recognize the bodily self, entailing the identification of visual features and/or the sensorimotor information (Ferri et al., 2012; Frassinetti et al., 2011; Tsakiris, 2010).

The specificity observed for self-hand recognition in our data suggests that the self has a systematic processing advantage, likely related to its inherent multimodal dimension. Differently from images depicting others' bodies, which cannot be felt, visual stimuli representing the bodily-self have immediate access also to sensorimotor information, thus enriching their representation and salience. The present results, therefore, are compatible with the idea of an integrated, multisensory network devoted to the recognition of the bodily-self (Limanowski & Blankenburg, 2015, 2016; Zeller et al., 2016). The visual representation of body effectors, besides primary visual cortices, may activate a circuit of sensorimotor areas (including the ventral-premotor cortex) and of extrastriate, associative visual cortices (such as the extrastriate body area – EBA – in the temporal lobe) (Ferri et al., 2012; Frassinetti et al., 2011; Limanowski al., 2018). However, how can this multimodal activity be observed? Recently, a novel EEG paradigm has been specifically designed to highlight the sensorimotor activity in response to visual body recognition (Galvez-Pol al., 2020). EEG responses to bodily-self visual information should be recorded either in isolation (visual-only condition) or in combination with task-irrelevant motor and somatosensory events (multimodal condition). Then, the activation recorded in visual-only condition should be subtracted from the multimodal condition. This subtraction should highlight the supposed contribution of sensorimotor activity in response to bodily-self images. In the present study, we demonstrate that the implicit self-body recognition boosts the change detection and we postulate that this enhanced mechanism is related to the activation of a multimodal sensorimotor network devoted to the recognition of the bodily-self. To test this hypothesis in the next Chapter we will exploit such a multimodal EEG paradigm in the context of visual mismatch detection protocols. Parallelly, in Chapter 3 we will investigate the contribution of visuo-sensorimotor associations in driving bodily-self recognition by capitalizing on brain-damaged patients that show a disconnection within the fronto-parietal network.

1.5 References

Alzueta, E., Melcon, M., Poch, C., & Capilla, A. (2019). Is your own face more than a highly familiar face? Biol Psychol, 142, 100-107. doi: 10.1016/j.biopsycho.2019.01.018

Apps, M. A., & Tsakiris, M. (2014). The free-energy self: a predictive coding account of self-recognition. Neurosci Biobehav Rev, 41, 85-97. doi: 10.1016/j.neubiorev.2013.01.029

Bennett, M. A., Duke, P. A., & Fuggetta, G. (2014). Event-related potential N270 delayed and enhanced by the conjunction of relevant and irrelevant perceptual mismatch. Psychophysiology, 51(5), 456-463. doi: 10.1111/psyp.12192

Botvinick, M., & Cohen, J. (1998). Rubber hands 'feel' touch that eyes see. Nature, 391(6669), 756. doi: 10.1038/35784

Bruno, V., Ronga, I., Fossataro, C., Capozzi, F., & Garbarini, F. (2019). Suppressing movements with phantom limbs and existing limbs evokes comparable electrophysiological inhibitory responses. Cortex, 117, 64-76. doi: 10.1016/j.cortex.2019.02.024

Bruno, V., Ronga, I., Fossataro, C., Galigani, M., Sacco, K., & Garbarini, F. (2020). Long-term limb immobilization modulates inhibition-related electrophysiological brain activity. Neuroimage, 218, 116911. doi: 10.1016/j.neuroimage.2020.116911

Bucchioni, G., Fossataro, C., Cavallo, A., Mouras, H., Neppi-Modona, M., & Garbarini, F. (2016). Empathy or Ownership? Evidence from Corticospinal Excitability Modulation during Pain Observation. J Cogn Neurosci, 28(11), 1760-1771. doi: 10.1162/jocn_a_01003

Burin, D., Garbarini, F., Bruno, V., Fossataro, C., Destefanis, C., Berti, A., & Pia, L. (2017). Movements and body ownership: Evidence from the rubber hand illusion after mechanical limb immobilization. Neuropsychologia, 107, 41-47. doi: 10.1016/j.neuropsychologia.2017.11.004

Butler, D. L., Mattingley, J. B., Cunnington, R., & Suddendorf, T. (2013). Different neural processes accompany self-recognition in photographs across the lifespan: an ERP study using dizygotic twins. PLoS One, 8(9), e72586. doi: 10.1371/journal.pone.0072586

Caharel, S., d'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: evidence from the N170 ERP component. Neuropsychologia, 47(3), 639-643. doi: 10.1016/j.neuropsychologia.2008.11.016

Cardini, F., Costantini, M., Galati, G., Romani, G. L., Ladavas, E., & Serino, A. (2011). Viewing one's own face being touched modulates tactile perception: an fMRI study. J Cogn Neurosci, 23(3), 503-513. doi: 10.1162/jocn.2010.21484

Conson, M., Errico, D., Mazzarella, E., De Bellis, F., Grossi, D., & Trojano, L. (2015). Impact of body posture on laterality judgement and explicit recognition tasks performed on self and others' hands. Exp Brain Res, 233(4), 1331-1338. doi: 10.1007/s00221-015-4210-3

Conson, M., Volpicella, F., De Bellis, F., Orefice, A., & Trojano, L. (2017). "Like the palm of my hands": Motor imagery enhances implicit and explicit visual recognition of one's own hands. Acta Psychol (Amst), 180, 98-104. doi: 10.1016/j.actpsy.2017.09.006

De Bellis, F., Trojano, L., Errico, D., Grossi, D., & Conson, M. (2017). Whose hand is this? Differential responses of right and left extrastriate body areas to visual images of self and others' hands. Cogn Affect Behav Neurosci, 17(4), 826-837. doi: 10.3758/s13415-017-0514-z

Della Gatta, F., Garbarini, F., Puglisi, G., Leonetti, A., Berti, A., & Borroni, P. (2016). Decreased motor cortex excitability mirrors own hand disembodiment during the rubber hand illusion. Elife, 5. doi: 10.7554/eLife.14972

Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. J Neurosci, 25(45), 10564-10573. doi: 10.1523/JNEUROSCI.0800-05.2005

Enriquez-Geppert, S., Konrad, C., Pantev, C., & Huster, R. J. (2010). Conflict and inhibition differentially affect the N200/P300 complex in a combined go/nogo and stop-signal task. Neuroimage, 51(2), 877-887. doi: 10.1016/j.neuroimage.2010.02.043

Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2010). Detecting novelty and significance. J Cogn Neurosci, 22(2), 404-411. doi: 10.1162/jocn.2009.21244

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A sensorimotor network for the bodily self. J Cogn Neurosci, 24(7), 1584-1595. doi: 10.1162/jocn_a_00230

Ferri, F., Frassinetti, F., Costantini, M., & Gallese, V. (2011). Motor simulation and the bodily self. PLoS One, 6(3), e17927. doi: 10.1371/journal.pone.0017927

Folstein, J. R., & Van Petten, C. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: a review. Psychophysiology, 45(1), 152-170. doi: 10.1111/j.1469-8986.2007.00602.x

Fossataro, C., Bruno, V., Giurgola, S., Bolognini, N., & Garbarini, F. (2018). Losing my hand. Body ownership attenuation after virtual lesion of the primary motor cortex. Eur J Neurosci, 48(6), 2272-2287. doi: 10.1111/ejn.14116

Fossataro, C., Bucchioni, G., D'Agata, F., Bruno, V., Morese, R., Krystkowiak, P., & Garbarini, F. (2018). Anxiety-dependent modulation of motor responses to pain expectancy. Soc Cogn Affect Neurosci. doi: 10.1093/scan/nsx146

Frassinetti, F., Ferri, F., Maini, M., Benassi, M. G., & Gallese, V. (2011). Bodily self: an implicit knowledge of what is explicitly unknown. Exp Brain Res, 212(1), 153-160. doi: 10.1007/s00221-011-2708-x

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. J Cogn Neurosci, 20(8), 1507-1516. doi: 10.1162/jocn.2008.20067

Frassinetti, F., Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., . . . Farne, A. (2009). Visual processing of moving and static self body-parts. Neuropsychologia, 47(8-9), 1988-1993. doi: 10.1016/j.neuropsychologia.2009.03.012

Galigani, M., Ronga, I., Bruno, V., Castellani, N., Rossi Sebastiano, A., Fossataro, C., & Garbarini, F. (2021). Salience effects on visual change detection: face-like configurations modulate electrophysiological mismatch responses European Journal of Neuroscience.

Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2020). Revealing the body in the brain: An ERP method to examine sensorimotor activity during visual perception of body-related information. Cortex, 125, 332-344. doi: 10.1016/j.cortex.2020.01.017

Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. [Review]. Trends Cogn Sci, 10(1), 14-23. doi: 10.1016/j.tics.2005.11.006

Hu, C., Di, X., Eickhoff, S. B., Zhang, M., Peng, K., Guo, H., & Sui, J. (2016). Distinct and common aspects of physical and psychological self-representation in the brain: A meta-analysis of self-bias in facial and self-referential judgements. Neurosci Biobehav Rev, 61, 197-207. doi: 10.1016/j.neubiorev.2015.12.003

Iannetti, G. D., Hughes, N. P., Lee, M. C., & Mouraux, A. (2008). Determinants of laser-evoked EEG responses: pain perception or stimulus saliency? [Research Support, Non-U.S. Gov't]. J Neurophysiol, 100(2), 815-828. doi: 10.1152/jn.00097.2008

Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. [Clinical Trial Research Support, Non-U.S. Gov't

Research Support, U.S. Gov't, Non-P.H.S.]. Psychophysiology, 37(2), 163-178. doi: 10.1111/1469-8986.3720163

Legrain, V., Iannetti, G. D., Plaghki, L., & Mouraux, A. (2011). The pain matrix reloaded: a salience detection system for the body. [Research Support, Non-U.S. Gov't Review]. Prog Neurobiol, 93(1), 111-124. doi: 10.1016/j.pneurobio.2010.10.005

Li, L., Wang, Y., Wang, H., Cui, L., & Tian, S. (2003). Event-related potential N270 and its distribution in adults and school-age children. Brain Dev, 25(7), 507-513. doi: 10.1016/s0387-7604(03)00059-7

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. Hum Brain Mapp, 36(6), 2284-2304. doi: 10.1002/hbm.22770

Limanowski, J., & Blankenburg, F. (2016). That's not quite me: limb ownership encoding in the brain. Soc Cogn Affect Neurosci, 11(7), 1130-1140. doi: 10.1093/scan/nsv079

Limanowski, J., Sarasso, P., & Blankenburg, F. (2018). Different responses of the right superior temporal sulcus to visual movement feedback during self-generated vs. externally generated hand movements. Eur J Neurosci, 47(4), 314-320. doi: 10.1111/ejn.13824

Longo, M. R., Schuur, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. Acta Psychol (Amst), 132(2), 166-172. doi: 10.1016/j.actpsy.2009.02.003

Morita, T., Saito, D. N., Ban, M., Shimada, K., Okamoto, Y., Kosaka, H., . . . Naito, E. (2018). Self-Face Recognition Begins to Share Active Region in Right Inferior Parietal Lobule with Proprioceptive Illusion During Adolescence. Cereb Cortex, 28(4), 1532-1548. doi: 10.1093/cercor/bhy027

Mouraux, A., Diukova, A., Lee, M. C., Wise, R. G., & Iannetti, G. D. (2011). A multisensory investigation of the functional significance of the "pain matrix". [Research Support, Non-U.S. Gov't]. Neuroimage, 54(3), 2237-2249. doi: 10.1016/j.neuroimage.2010.09.084

Mouraux, A., & Iannetti, G. D. (2008). Across-trial averaging of event-related EEG responses and beyond. [Research Support, Non-U.S. Gov't Review]. Magn Reson Imaging, 26(7), 1041-1054. doi: 10.1016/j.mri.2008.01.011

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. Neuroimage, 42(4), 1669-1677. doi: 10.1016/j.neuroimage.2008.05.045

Pia, L., Fossataro, C., Burin, D., Bruno, V., Spinazzola, L., Gindri, P., . . . Garbarini, F. (2020). The anatomo-clinical picture of the pathological embodiment over someone else's body part after stroke. Cortex, 130, 203-219. doi: 10.1016/j.cortex.2020.05.002

Ronga, I., Sarasso, P., Fossataro, C., Salatino, A., Garbarini, F., Ricci, R., & Neppi-Modona, M. (2018). Everything is illuminated: Prismatic adaptation lowers visual detection threshold in normal subjects. J Exp Psychol Hum Percept Perform, 44(10), 1619-1628. doi: 10.1037/xhp0000559

Ronga, I., Valentini, E., Mouraux, A., & Iannetti, G. D. (2013). Novelty is not enough: laser-evoked potentials are determined by stimulus saliency, not absolute novelty. [Research Support, Non-U.S. Gov't]. Journal of Neurophysiology, 109(3), 692-701. doi: 10.1152/jn.00464.2012

Sarasso, P., Ninghetto, M., Salatino, A., Ronga, I., Bongiardina, A., Iarrobino, I., . . . Ricci, R. (2018). Everything is (still) illuminated: Dual right cathodal-left anodal tDCS of PPC prevents fatigue on a visual detection task. Brain Stimul. doi: 10.1016/j.brs.2018.09.017

Sarasso, P., Ronga, I., Pistis, A., Forte, E., Garbarini, F., Ricci, R., & Neppi-Modona, M. (2019). Aesthetic appreciation of musical intervals enhances behavioural and neurophysiological indexes of attentional engagement and motor inhibition. Sci Rep, 9(1), 18550. doi: 10.1038/s41598-019-55131-9

Scannella, S., Pariente, J., De Boissezon, X., Castel-Lacanal, E., Chauveau, N., Causse, M., . . . Pastor, J. (2016). N270 sensitivity to conflict strength and working memory: A combined ERP and sLORETA study. Behav Brain Res, 297, 231-240. doi: 10.1016/j.bbr.2015.10.014

Schweinberger, S. R., & Neumann, M. F. (2016). Repetition effects in human ERPs to faces. Cortex, 80, 141-153. doi: 10.1016/j.cortex.2015.11.001

Sugiura, M. (2015). Three faces of self-face recognition: potential for a multi-dimensional diagnostic tool. Neurosci Res, 90, 56-64. doi: 10.1016/j.neures.2014.10.002

Tanaka, J. W., & Pierce, L. J. (2009). The neural plasticity of other-race face recognition. Cogn Affect Behav Neurosci, 9(1), 122-131. doi: 10.3758/CABN.9.1.122

Torta, D. M., Liang, M., Valentini, E., Mouraux, A., & Iannetti, G. D. (2012). Dishabituation of laser-evoked EEG responses: dissecting the effect of certain and uncertain changes in stimulus spatial location. Experimental Brain Research. doi: 10.1007/s00221-012-3019-6

Tsakiris, M. (2008). Looking for myself: current multisensory input alters self-face recognition. PLoS One, 3(12), e4040. doi: 10.1371/journal.pone.0004040

Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-ownership. Neuropsychologia, 48(3), 703-712. doi: 10.1016/j.neuropsychologia.2009.09.034

Valentini, E., Torta, D. M., Mouraux, A., & Iannetti, G. D. (2011). Dishabituation of laser-evoked EEG responses: dissecting the effect of certain and uncertain changes in stimulus modality. [Research Support, Non-U.S. Gov't]. J Cogn Neurosci, 23(10), 2822-2837. doi: 10.1162/jocn.2011.21609

Wang, A. L., Mouraux, A., Liang, M., & Iannetti, G. D. (2010). Stimulus novelty, and not neural refractoriness, explains the repetition suppression of laser-evoked potentials. [Comparative Study

Research Support, Non-U.S. Gov't]. J Neurophysiol, 104(4), 2116-2124. doi: 10.1152/jn.01088.2009

Wang, P., Tan, C. H., Li, Y., Zhang, Q., Wang, Y. B., & Luo, J. L. (2018). Event-related potential N270 as an index of social information conflict in explicit processing. Int J Psychophysiol, 123, 199-206. doi: 10.1016/j.ijpsycho.2017.03.005

Wang, Y., Cui, L., Wang, H., Tian, S., & Zhang, X. (2004). The sequential processing of visual feature conjunction mismatches in the human brain. Psychophysiology, 41(1), 21-29. doi: 10.1111/j.1469-8986.2003.00134.x

Wang, Y., Tian, S., Wang, H., Cui, L., Zhang, Y., & Zhang, X. (2003). Event-related potentials evoked by multi-feature conflict under different attentive conditions. Exp Brain Res, 148(4), 451-457. doi: 10.1007/s00221-002-1319-y

Zeller, D., Friston, K. J., & Classen, J. (2016). Dynamic causal modeling of touch-evoked potentials in the rubber hand illusion. Neuroimage, 138, 266-273. doi: 10.1016/j.neuroimage.2016.05.065

Zhang, X., Ma, L., Li, S., Wang, Y., Weng, X., & Wang, L. (2008). A mismatch process in brief delayed matching-to-sample task: an fMRI study. Exp Brain Res, 186(2), 335-341. doi: 10.1007/s00221-008-1285-0

Chapter 2. The tactile knowledge of the visual bodily-self

[This research was conducted in collaboration with Prof. Bettina Forster, Department of Psychology, City University of London. At the time of the writing of the present thesis, these data are unpublished]

2.1 Introduction

In Chapter 1, we identified an electrophysiological correlate of self-advantage by showing that mismatch detection phenomenon is boosted by implicit self-hand recognition. Indeed, when the change involved the self-hand, we observed a greater amplitude of N270 component than when the other-hand was presented. This result suggests that the own hand is perceived as more salient by our brain and that the implicit recognition of the self-hand recruit different neural mechanisms and networks than the other-hand. Hence, the next step of this line of research consists of the investigation of the brain dynamics subserving bodily-self recognition.

Recently, influential views posited that we may resort sensorimotor information (e.g., somatosensory, visual, proprioceptive, and motor) to recognize our own body effectors, whereas we usually distinguish other people's bodies by vision only (Ferri et al., 2012a; Frassinetti et al., 2009; Myers & Sowden, 2008). More specifically, the self-advantage may be associated with the activation of a visual-sensorimotor network including, besides occipital areas, bilateral premotor cortex and right temporal cortex encompassing the extrastriate body area (Ferri et al., 2012a). However, even though the study by Ferri and colleagues revealed a direct involvement of the somatosensory cortices in self-hand recognition, since a motor task (i.e., hand-rotation) was performed, it cannot be excluded that the (motor) nature of the task might have contributed to the observed sensorimotor activation.

The idea that bodily-self recognition implies the interaction between visual and sensorimotor areas has been confirmed also by different lines of research that does not employ motor tasks, such as those studies investigating the neural correlates of a famous illusion of body ownership (Botvinick & Cohen, 1998; della Gatta et al., 2016; Fossataro, Bruno, Giurgola, et al., 2018). During this illusion, participants, while watching a human-like rubber hand being touched synchronously with their own hand hidden from view, experience the feeling that the fake hand has become part of their own body. It has been demonstrated that, during this procedure, the functional connectivity between visual areas (e.g. lateral occipitotemporal cortex and extrastriate body area; EBA) and ventral premotor cortex is specifically modulated during the embodiment (i.e. when the fake hand is attributed to themselves) (Limanowski & Blankenburg, 2015; Zeller et al., 2016), consistently with the fact that the illusion reduces the perceived objective (visual) dissimilarities between the own and the rubber hand (Longo et al., 2009). Moreover, lesion studies of brain damaged patients exhibiting an impairment of self-other hands discrimination support the involvement of a visual-sensorimotor network in self-recognition. Indeed, the core lesion underpinning this deficit has been identified in the subcortical white matter connecting temporal areas, involved in the visual recognition of the body (i.e., the extrastriate body area, EBA), with anterior multisensory areas, such as the premotor cortex (Errante et al., 2022).

Furthermore, the recruitment of multimodal networks (including sensorimotor areas) in self-recognition is not only observed for limb discrimination, but it has been described for faces as well, without the involvement of a motor task (Cardini et al., 2011; Sugiura et al., 2015). For example, Cardini and colleagues found that ventral premotor cortex activity differed when viewing self-face as compared to another's face, thus revealing a crucial role of sensorimotor areas in self-other face discrimination. Accordingly, the processing of the self-face has been associated to a specific sensorimotor pattern of activations, involving sensory (i.e., visual, somatosensory and interoceptive areas) and motor association cortices (i.e., premotor cortex and supplementary motor area – see Sugiura et al., 2015 for a review). Overall these findings suggest the presence of different mechanisms for self- versus other people's body recognition (De Bellis et al., 2017; Ferri et al., 2012a; Myers & Sowden, 2008), thus highlighting the specificity of self-recognition.

In this work we investigated whether the somatosensory cortex plays a crucial role in implicit self-hand recognition. To test the somatosensory account for the identification of own body effectors, we leveraged a validated electrophysiological approach, which entails the subtraction of visual activity from visual-tactile activity (Arslanova et al., 2019; Galvez-Pol et al., 2018, 2020; Sel et al., 2014). In this way, you can obtain the so-called Vep-free Sep, which is a somatosensory potential cleaned by visual artifacts. Therefore, this method allows examining visually-driven processing of information in cortices other than visual areas, specifically over the somatosensory cortex. In this protocol, visual bodily stimuli are presented and in the half of the trials a task-irrelevant tactile stimulation is concomitantly delivered to index fingers. By subtracting visual from visual-tactile activity it is possible to unveil the contribution of somatosensory cortex during a visual task.

In Experiment 1, we used a very similar paradigm to that of Chapter 1 and we presented images of hands belonging either to the participants (Self) or to other people (Other1, Other2, Other3). Visual stimuli could be either identical or different and they were administered in two scenarios (i.e., With Self and Without Self scenario), depending on whether the self-hand was included in the pair. On half of the trials participants received a brief task-irrelevant tactile stimulation to the index fingers of both hands at the onset of the visual stimuli. In Experiment 2, we aimed at replicating the results of Experiment 1 by introducing a 50 ms delay between the visual and the tactile stimulus in visuo-tactile trials. In this way, we wanted to align the cortical processing of the two stimuli; indeed, based on physiological studies on monkeys, we know that that tactile stimuli are faster then visual ones to reach the cortex (Musacchia & Schroeder, 2009), this may not have allow the visual stimulus to directly affect somatosensory cortex activity, but just associative secondary areas. Hence, if somatosensory cortex actively contributes to self-hand recognition, we should observe greater Vep-free Seps when the self-hand is presented as compared to when the other-hand is shown. Conversely, if we will observe similar somatosensory activity evoked by the presentation of the self and the other hand, this would challenge the idea of a role of somatosensory information in sustaining bodily-self recognition.

2.2 Materials and Methods

2.2.1 Experiment 1 (discovery sample)

2.2.1.1 Participants

Eighteen healthy right-handed subjects participated in the study (women: 10; years: mean ± SD= 26.1 ± 3.1; years of education: mean ± SD= 17.6 ± 0.8). All subjects had normal (self-reported) or corrected to normal vision. All the participants signed the informed consent. The study conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 125055, 12/07/16).

2.2.1.2 Stimuli and Experimental Design

Visual stimuli consisted of grey-scale pictures (10 * 15 cm) of the dorsum of right hands belonging either to the participants or to other people. We took the picture of hands before the experiment, all in the same room and with controlled illumination conditions. We post-processed the images by removing and replacing the background with a black uniform one. Then, we converted original color pictures into grey-scale images to standardize different skin colors. Finally, we resized hand images to have all similar dimensions. The resulting visual stimuli were displayed using E-Prime2 Software (Psychology Software Tools, Pittsburgh, PA) for 300 ms at the center of a 21-inch Sony CRT computer screen.

On half of the trials, in addition to the image of hands, participants received a brief task-irrelevant tactile stimulation concurrently to the index fingers of both hands in order to elicit somatosensory evoked activity. Tactile stimulation were brief (200 μs) transcutaneous electrical stimuli consisting in constant current square-wave pulses (DS7A, Digitimer) delivered to the index finger of both hands. The stimulation intensity was adjusted according to the individual sensory threshold [estimated using the methods of limits 2, as in previous studies 3,5]. The mean (± SD) bilateral threshold stimulus intensity was 3.39 ± 1.12 mA, range

1.88–7 mA. During the experiment, the stimulation intensity was set slightly above the threshold (stimulation intensity = threshold intensity*2), so that participants always perceived the tactile stimulation, which was never painful.

The experimental paradigm (presented in Fig. 4) partially replicated the methodology proposed by Galigani et al. (2021). The experiment consisted of two scenarios (i.e., With Self and Without Self scenarios), administered in two different sessions. The order of the two sessions was counterbalanced between subjects, so that one half of the participants started with the With Self scenario, whereas the other half with the Without Self scenario. In each scenario, we presented pairs of visual stimuli (vS1 and vS2), delivered at a constant 1-sec inter-stimulus interval. The inter-trial interval between each pair was randomly jittered between 3.5 and 4.5 sec, in a way that participants could not anticipate stimulus occurrence.

In both scenarios, vS1 and vS2 could be either identical or different. In the With Self scenario, participants' self-hand was included. We presented four different pairs: Self-Self (with both vS1 and vS2 depicting the self- hand); Other1-Other1 (with vS1 and vS2 depicting the same hand belonging to a stranger - Other1); Self-Other1 (with vS1 representing the self-hand and vS2 the stranger hand); Other1-Self (with vS1 representing the stranger hand and vS2 the self-hand). In the Without Self scenario, the self-hand was never included and we delivered four different pairs: Other2- Other2 (with vS1 and vS2 depicting the same hand belonging to a stranger - Other2, different from Other1); Other3-Other3 (with both vS1 and vS2 depicting the same hand belonging to a stranger - Other3, different from Other1 and Other2); Other2- Other3 (with vS1 representing Other2's hand and vS2 Other3's hand); Other3-Other2 (with vS1 representing Other3's hand and vS2 Other2's hand). Notably, in both scenarios we matched the others' hands for the gender of participants.

Each scenario was composed of eight 8-minutes recording blocks and each block consisted of 80 pairs of visual stimuli. On half of all trials only VEPs were elicited in response to the onset of both the visual stimuli at the start of each trial (i.e., visual-only trials). On the other half of the trials VEPs and SEP's were elicited simultaneously by applying task-irrelevant single tactile probes concurrently to both images to the participants' index fingers of both hands (i.e., visual-tactile trials). Overall, participants performed a total of 640 trials; this equals 160 trials (80 visual-only and 80 visual-tactile) for each condition.

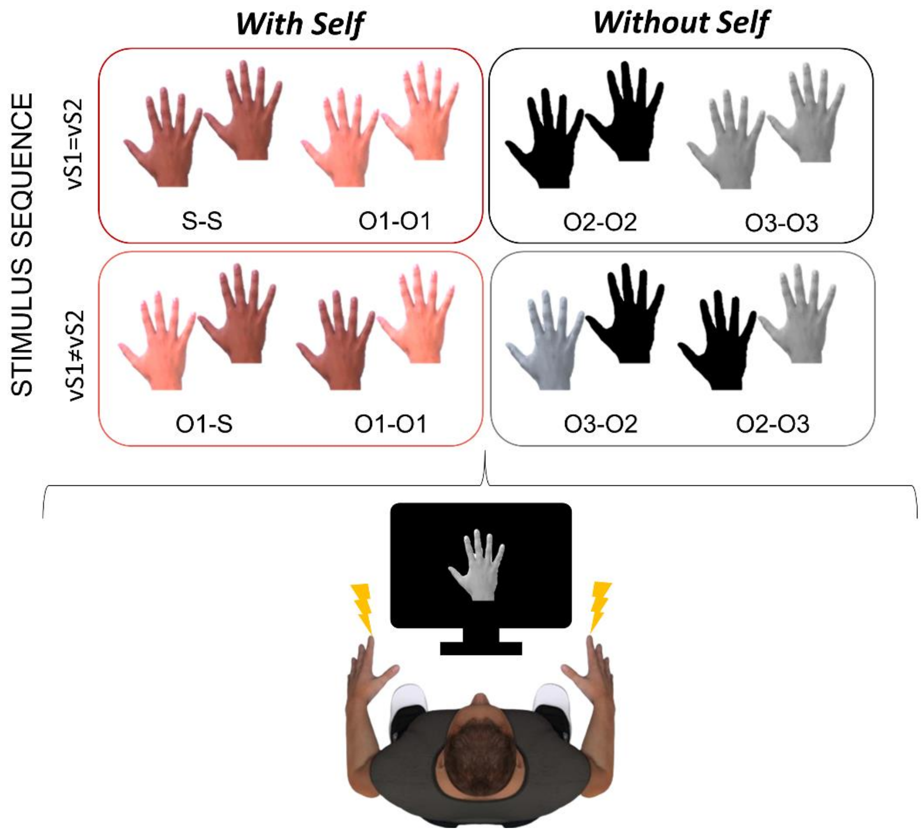


Figure 4. Experimental paradigm of Experimental 1. The experiment was divided into two different scenarios: With Self (where the self-hand was included), and Without Self (where the self-hand was never presented). On the half of the trials participants were presented with visual trials and on the other half with visual-tactile trials.

2.2.1.3 Behavioral task and EEG recording

During the experiment, participants were comfortably seated in a e chair in a silent, dimly lit room, at a distance of 55 cm from the computer screen. They were asked to focus on the stimuli and look at a fixation cross, placed at the center of the screen. The task consisted of deciding whether the vS2 was identical or different as compared to vS2, and RTs and accuracy of verbal responses were recorded.

During the matching task, ERPs were recorded using 32 Ag- AgCl active electrodes mounted on the scalp according to the International 10–20 system and referenced to the nose. Electrode impedances were kept below 5 kΩ. To track ocular movements and eye blinks, the electrooculogram was recorded placing two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Continuous EEG was recorded using a HandyEEG-SystemPLUS Evolution amplifier (Micromed) and a 1,024 Hz sampling rate.

2.2.1.4 Data Analysis

Behavioral data. Subjects' RTs for each pair type were collected and averaged. Importantly, trials with individual RTs exceeding two standard deviations below or above the mean (of each specific experimental condition) as well as trials with missing or wrong response were discarded from RT analysis (Conson et al., 2015; Ronga et al., 2018; Sarasso et al., 2019). The average number of discarded responses per participant was around 5%. In order to explore the presence of the self-advantage effect in our matching task, we performed two (on per each scenario) 2*2 repeated measures ANOVAs on RTs as dependent variables, with two within-subject factors: "Sequence" (two levels: S1=S2, S1≠S2) and "Identity" (related to the second stimulus of the pair; two levels: self, other). The normal distribution of residuals was checked by using Shapiro-Wilk's test (p always > 0.05). To explore significant interactions, ad hoc planned comparisons were performed and corrected with Bonferroni's test. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

Electrophysiological data. EEG data were pre-processed using Letswave v.6 (http:// www.nocions.org/letswave/, Mouraux & Iannetti, 2008). The EEG signal was epoched into segments lasting from 100 ms before to 500 ms after the stimulus (both for the analysis of vS1 and vS2 - total epoch duration: 600 ms). Segments were band-pass filtered (0.05–30 Hz) using a fast Butterworth filter (4th order), and then baseline corrected to the first 100 ms. Artifacts due to eye blinks and eye movements were subtracted using a validated method based on an Independent Component Analysis [ICA – 10]. Blinks were found to be the most frequent cause of rejection. Finally, grand averages were computed separately for each condition and for visual-only and visual-tactile trials.

We adopted a statistical approach that estimates possible effects over the whole epoch time-course. We performed a point-by-point analysis that quantify significant effects at all time points and electrodes and highlight significantly different ERP time windows among different experimental conditions. Importantly, the analysis is performed on each electrode separately. Since the present statistical approach performs one comparison per time point, it has to be corrected for multiple comparisons. With this aim, all the reported point-by-point analyses are corrected through a cluster-based permutation test (1000 permutations). The same statistical approach (point-by-point analyses combined with permutation testing as a correction for multiple comparisons) has been repeatedly employed in recent EEG studies (Bruno et al., 2019; Harris et al., 2018; Novembre et al., 2018; Ronga et al., 2013; Sarasso et al., 2020; Vuilleumier et al., 2017).

Importantly, our analysis focused both on the first and the second stimulus, and we investigated visual evoked activity and somatosensory evoked activity. In order to uncover the involvement of the somatosensory cortex in self-hand recognition, we adopted a previous approach (Arslanova et al., 2019; Galvez-Pol et al., 2018, 2020; Sel et al., 2014) consisting on subtracting the visual-only trials from visual-tactile trials. This subtraction dissociates neural evoked activity in somatosensory areas during visual processing, over and above a potential carry-over of activity from VEPs. Therefore, this method allows the possibility of examining visually driven processing of information in cortices other than visual areas, specifically over SCx. If self-hand recognition relies on somatosensory processing, then tactually probed SCx response should be differentially affected depending on whether self-hand or other's hand were presented.

First stimulus. To analyze visual and somatosensory activity evoked by the first stimulus of the pair, we firstly averaged the conditions with the same first stimulus (e.g., S-S with S-O1), thus yielding two conditions per scenario (With Self: S, O1; Without Self: O2, O3). In each scenario, we performed two point-by-point t-tests (corrected with 1000 permutations) to respectively compare visual-evoked activity and somatosensory evoked activity.

Second stimulus. To analyze visual and somatosensory activity evoked by the second stimulus of the pair, in each scenario we run a 2*2 point-by-point, repeated-measures ANOVA with "Sequence" (two levels: S1=S2, S1≠S2) and "Identity" (two levels: Self, Other1 in the With Self Scenario; Other2, Other3 in the Without Self Scenario) as within-subject factors. In order to correct for multiple comparison across time points, we employed permutation testing (1000 permutations). This analysis yielded three distinct waveforms, representing the significance of the main effect of the two factors across time, as well as their interaction.

2.2.2 Experiment 2 (replicating sample)

2.2.2.1 Participants

Eighteen healthy right-handed subjects participated in the study (women: 10; years: mean ± SD= 25.17 ± 2.9; years of education: mean ± SD= 17 ± 1.1). All subjects had normal (self-reported) or corrected to normal vision. All the participants signed the informed consent. The study conformed to the standards required by the Declaration of Helsinki and was approved by the Ethics Committee of the University of Torino (prot. n. 125055, 12/07/16).

2.2.2.2 Stimuli and Experimental Design

General procedures were identical to the Experiment 1, with the following exceptions. On visual-tactile trials, we included a 50 ms delay between the visual stimulus and the tactile stimulus to align the cortical processing of the two stimuli (Musacchia & Schroeder, 2009). Furthermore, we included only the With Self scenario.

2.2.2.3 Behavioral task and EEG recording

All procedures were identical to those of Experiment 1.

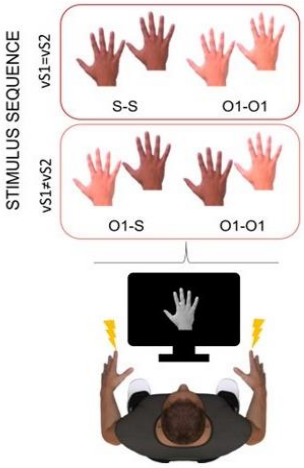


Figure 5. Experimental paradigm of Experimental 2. In this experiment only the With Self (where the self-hand was included) was presented. On the half of the trials participants were presented with visual trials and on the other half with visual-tactile trials.

2.2.2.4 Data Analysis

All the procedure for data pre-processing and data analysis were identical to those of Experiment 1, with the exception that we only focused on the analysis of the electrophysiological activity evoked by the presentation of the first stimulus of the pair.

2.3 Results

2.3.1 Experiment 1 (discovering sample)

2.3.1.1 Behavioral results

The 2*2 repeated measures ANOVA performed on RTs in the With Self scenario (Fig.6) revealed a significant Sequence*Identity Interaction ($F_{1,17}$=9,363; p=0.007; η2=0.355), thus suggesting that the facility in detecting changes in hand identity is modulated by the presence or not of the self-hand. Faster RTs were found in Self-Self pair (mean±SEM= 669.49±32.20 ms) as compared to Other1-Other1 pair (mean±SEM= 765.47±55.55 ms; p=0.032), Other1-Self pair (mean±SEM= 799.60± 60.69 ms; p=0.001) and Self-Other1 pair (mean±SEM= 783.39±62.34 ms; p=0.001).

The ANOVA in the Without Self scenario did not show any significant effect (all p*s*>0.21), thus confirming that the presence of others' hand does not affect the behavioral performance.

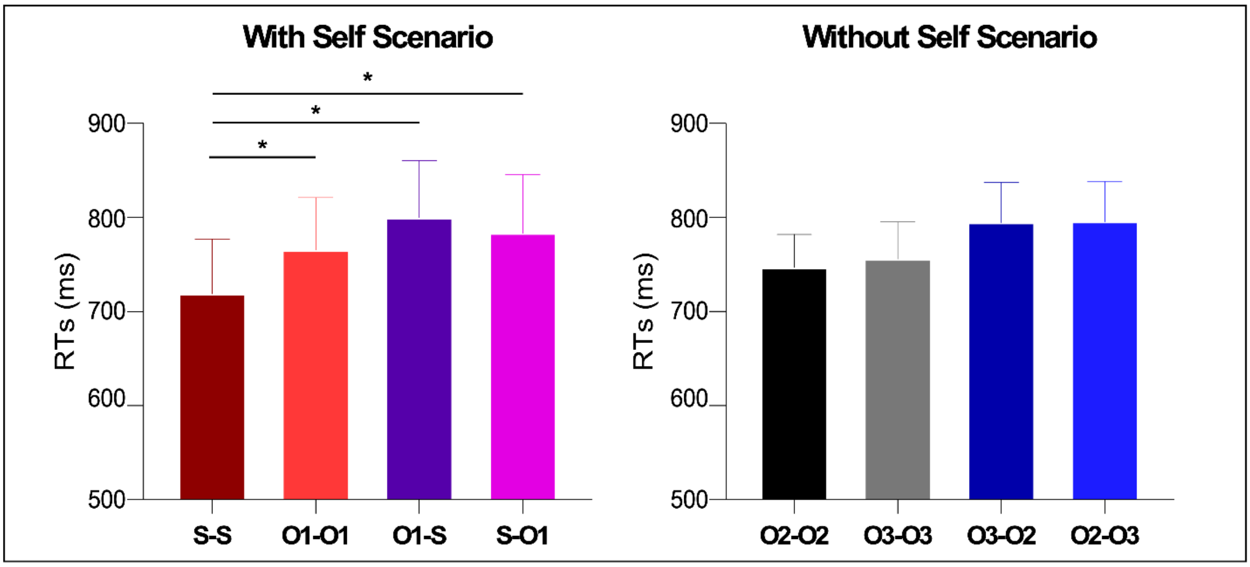


Figure 6. The figure represents the subjects' RTs. Note that subjects' performance was more faster anytime the self-hand was presented. We did not find any significant effect in the Without Self scenario.

2.3.1.2 Electrophysiological results

We investigated visual evoked activity and somatosensory evoked activity (isolated by subtracting the purely visually evoked activity from visual-tactile activity) elicited by both the first and second stimuli.

First stimulus. We investigated visual evoked activity and somatosensory evoked activity (isolated by subtracting the purely visually evoked activity from visual-tactile activity) elicited by both the first and second stimuli. When we compared visual activity elicited by the first stimulus (Fig.1X), we did not observe any significant difference between conditions, thus suggesting that visual evoked potentials are not affected by the identity of the hand (Self vs Other1: $t_{1,17}$ always < 0.43; Other2 vs Other3: $t_{1,17}$ always < 2.14). Crucially, we found that the visual presentation of the self-hand significantly magnified somatosensory activity as compared to the other-hand. In particular, the enhancement of somatosensory processing driven by self-hand recognition was present around SCx of both hemispheres but was maximal at Cp1 electrode from 127ms to 289 ms ($t_{1,17}$ = 4.50; p=0.0003), from 297ms to 361ms ($t_{1,17}$ = 2.73; p=0.014) and from 375 to 500 ms ($t_{1,17}$ = 3.54; p=0.002) after the stimulus onset. No significant differences emerged in the Without Self scenario ($t_{1,17}$ always< 2.12) (Fig.7).

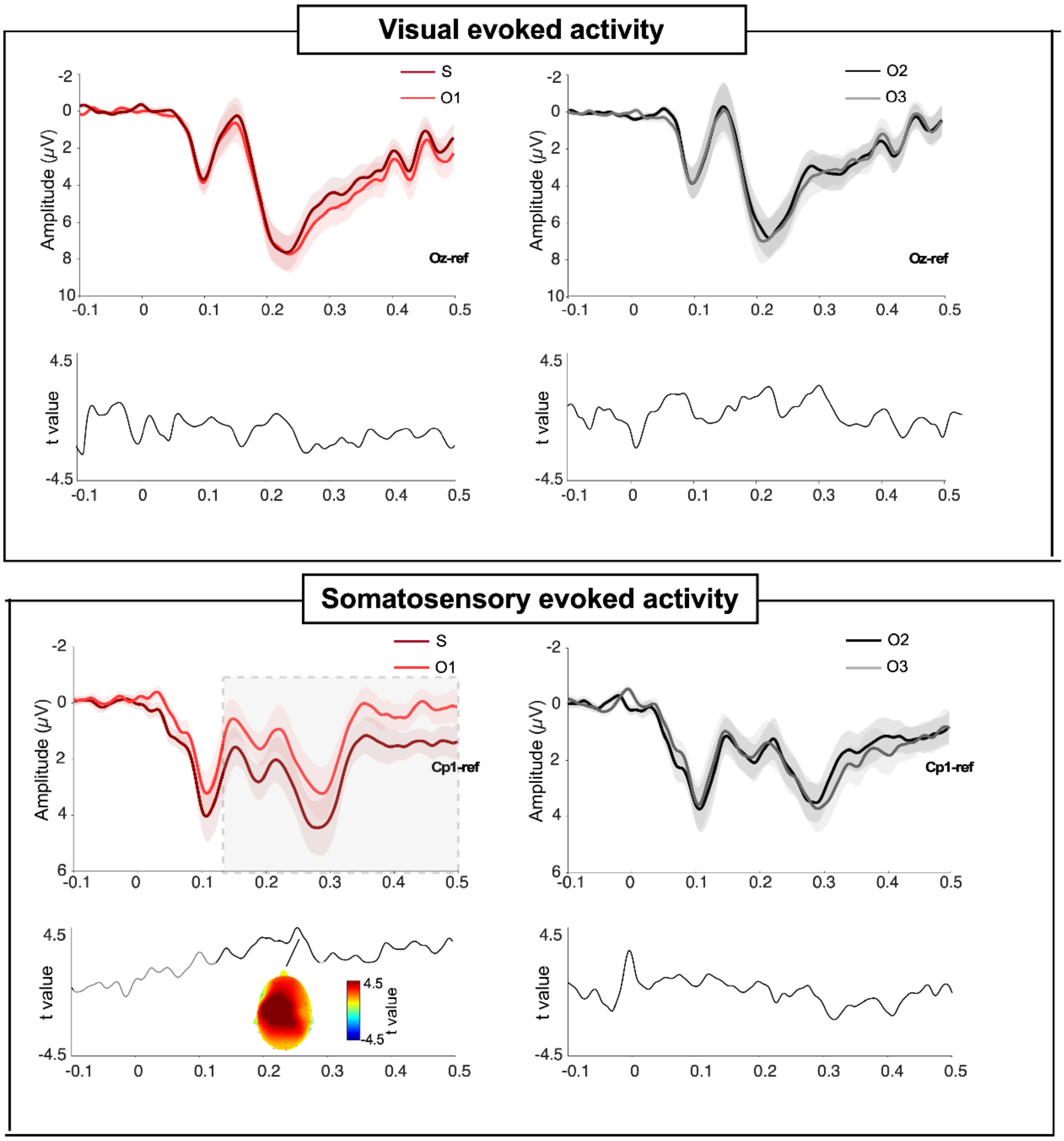


Figure 7. The top panel represents visual evoked activity in response to the first stimulus. The bottom panel represents somatosensory evoked activity in response to the first stimulus. Y axis: the mean voltage amplitude (μV); X axis: experimental conditions. Note that the With Self scenario is represented in red, while the Without Self scenario is represented in black.

Second stimulus. The point-by-point 2*2 ANOVA revealed that somatosensory evoked activity was greater in pairs of different as compared to pairs of identical stimuli in the With Self scenario (maximal at Cp1 electrode, latency: 95-139 ms post-stimulus, $F_{1,17} = 14.545$; $p = 0.001$) and not in the Without Self scenario ($F_{1,17}$ always < 1.713). Such effect suggests that the recognition of the self-hand triggered a sort of somatosensory change detection, by modulating tactile processing based on whether vS2 was preceded by an identical or different vS1. Interestingly, when analyzing visual evoked activity triggered by vS2, we replicated previous findings described in Chapter 1 that indicated that self-hand recognition enhanced visual change detection. We observed greater electrophysiological activity when vS2 was different than identical to vS1 in the With Self scenario (maximal at Fz electrode, latency: 225-281 ms post-stimulus; $F_{1,17} = 14.818$; $p = 0.001$; maximal at Pz, 313-421 ms post-stimulus; $F_{1,17} = 14.257$; $p = 0.002$), whereas in the Without Self scenario such difference emerged only at a later latency (maximal at FpZ electrode, latency: 384-474 ms post stimulus, $F_{1,17} = 34.785$; $p < 0.001$) (Fig.8).

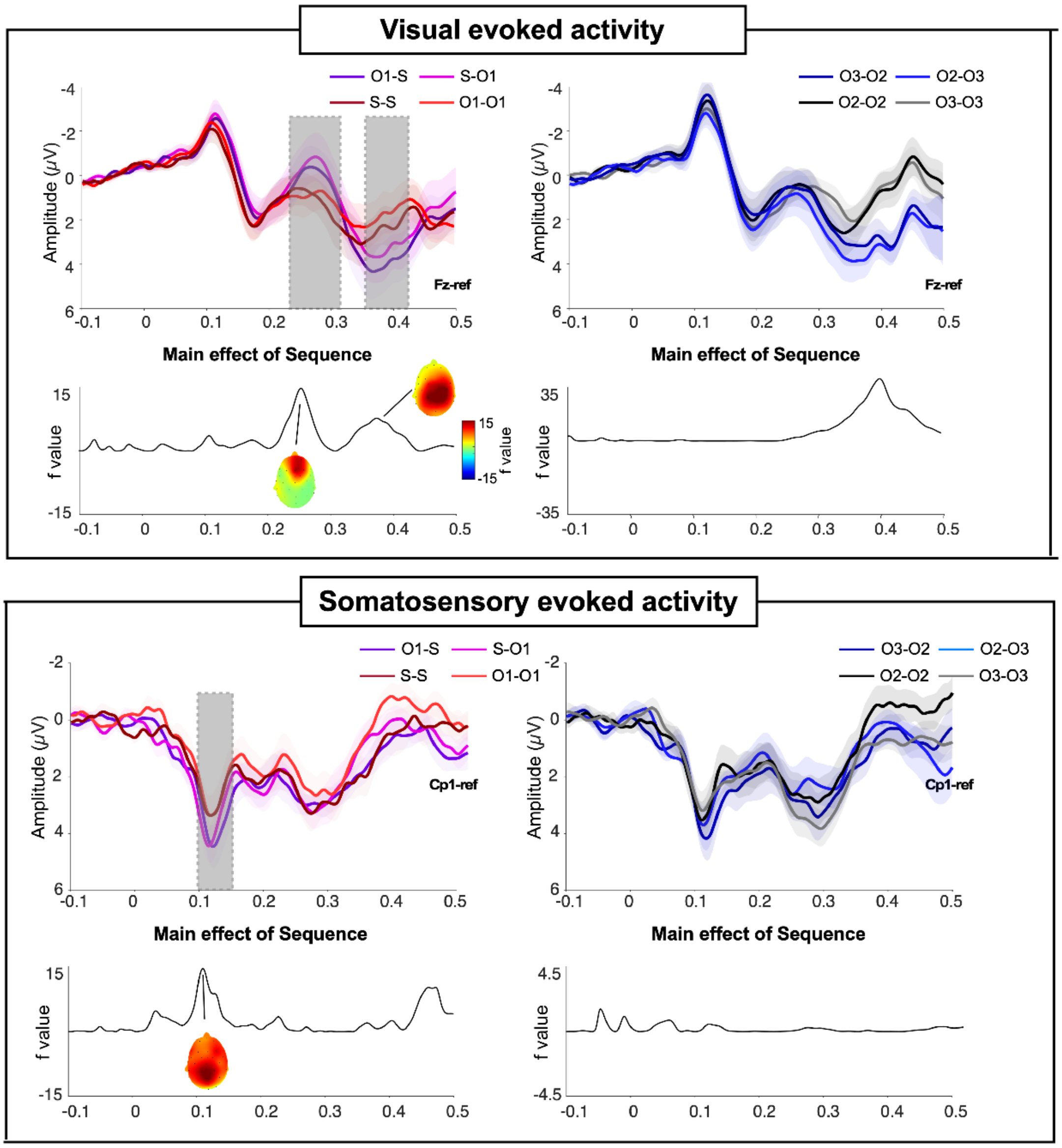


Figure 8. The top panel represents visual evoked activity in response to the second stimulus. The bottom panel represents somatosensory evoked activity in response to the second stimulus. Y axis: the mean voltage amplitude (μV); X axis: experimental conditions. Note that the With Self scenario is represented in red, while the Without Self Sequence is represented in blue. Shaded areas represent ERP sem.

2.3.2 Experiment 2 (replicating sample)

2.3.2.1 Electrophysiological results

We investigated visual evoked activity and somatosensory evoked activity (isolated by subtracting the purely visually evoked activity from visual-tactile activity) elicited by both the first stimulus. In Experiment 1, we found differences at around 100 ms and this may suggest the involvement of associative secondary areas and not of the primary somatosensory cortex. This effect can be due to the concomitance of visual and tactile stimulus. Indeed, the tactile stimulus reaches faster the cortex than the tactile one and delivering the stimuli at the same moment may have prevented to observe modulations of primary somatosensory cortex.

First stimulus. The point-by-point t-test on visual-evoked activity did not reveal any significant effect between the self-hand and the other hand ($t_{1,17}$ always < 1.19). Crucially, when comparing the somatosensory evoked activity we found greater activation elicited concomitantly with the presentation of the self-hand as compared to the other hand and such difference was maximal over Cp1 electrode between 42 e 80 ms ($t_{1,17} = 4.42$; p=0.0007) and between 153 e 261 ms ($t_{1,17} = 3.06$; p=0.0088) post stimulus. This earlier latency, with the respect to that Experiment 1, suggests a direct modulation of primary somatosensory cortex induced by the presentation of the self-hand (Fig.9).

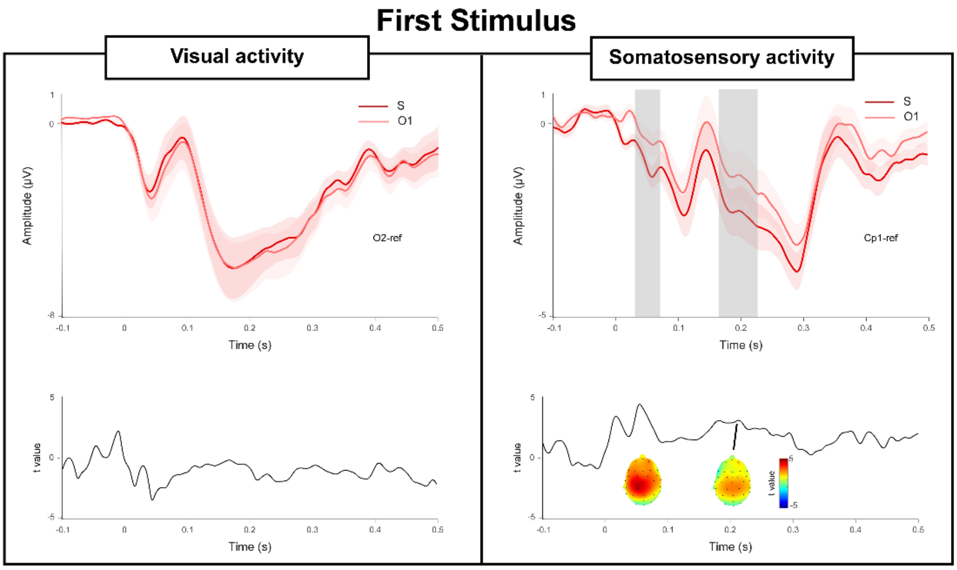


Figure 9. The figure represents visual (left panel) and somatosensory (right panrl) evoked activity in response to the first stimulus. Y axis: the mean voltage amplitude (μV); X axis: experimental conditions. Note that the With Self scenario is represented in red, while the Without Self scenario is represented in black. Shaded areas represent ERP sem.

2.4 Discussion

The present study, focused on bodily self-identification, explores the primary somatosensory cortex plays a role in the recognition of our physical identity. More specifically, we exploited the Veps-free Seps protocol (Arslanova et al., 2019; Galvez-Pol et al., 2020; Sel et al., 2014) to investigate whether the somatosensory evoked activity is modulated by the identity of the hand that is presented. Importantly, previous literature proposed that self-hand recognition may rely on sensorimotor representations, since it is supposed to recruit not only visual, but also sensorimotor brain networks (Apps & Tsakiris, 2014; Conson et al., 2017; Ferri et al., 2012a; Limanowski & Blankenburg, 2015).

In the following paragraphs we (1) describe our behavioral findings that further confirm the self-advantage effect also found in Chapter 1 and (2) discuss our electrophysiological results, which seem to show the involvement of somatosensory information in self-hand recognition. Importantly, the results highlighted in Experiment 1 (our discovering sample) were fully confirmed in Experiment 2, which, besides controlling for the timing of the arrival in cortex of visual and tactile stimuli, can be considered as a measure of internal replicability.

Our behavioral results confirmed the presence of the self-advantage in the same match-to sample task used also in (Galigani et al., 2021, see Chapter 1), thus further confirming the advantage in processing self than other's body effectors even though self-recognition is not explicitly required by experimental instructions (Conson et al., 2017; De Bellis et al., 2017; Frassinetti et al., 2008, 2009; Galigani et al., 2021). In Experiment 1, participants' RTs were selectively modulated in the With Self scenario, where we found that the presence of the self-hand in the pair fastened the behavioral performance. On the contrary, we did not observe any effect in the Without Self scenario, so, when the self-hand was not included in the pair, the RTs did not differ across conditions.

For what concerns the electrophysiological results, as suggest by previous literature (Ferri et al., 2012a; Galigani et al., 2021), we hypothesized a significantly different Vep-free Seps amplitude between self and other stimuli. The present data confirm our hypothesis (see below). Still, electrophysiological results in a way paralleled our behavioral findings, since in both experiments all significant modulations were selectively observed in the With Self scenario, thus pointing out the multimodal dimension of bodily-self recognition both from a behavioral and an electrophysiological point of view.

In Experiment 1, when we analyzed the visual activity evoked by the first stimulus of the pair, we found that that visual evoked potentials are not affected by the identity of the hand. This lack of modulation seems to reveal that the discrimination between the own and other's body is not charged to visual cortices, whose activation did not differ when it is presented the self hand or a stranger's hand. Crucially, we found that the visual presentation of the self-hand significantly magnified somatosensory activity as compared to the other-hand. Despite the tactile stimuli were the very same (for what concerns location, intensity and duration) across conditions, somatosensory evoked potential were greater when tactile stimuli were coupled with the image of the own hand than the image of an other's hand. Our differential effect was presented at around 100 ms post-stimulus, and this middle-late latency may reflect the activity of secondary associative areas and not directly the activity of primary somatosensory cortex. To disentangle between this possibilities, we replicated our paradigm (Experiment 2), by introducing a 50 ms delay between the visual and tactile stimulus. In this way, we wanted to align the cortical processing of the two stimuli; indeed, based on physiological studies on monkeys, we know that that tactile stimuli are faster then visual ones to reach the cortex (Musacchia & Schroeder, 2009), and this may not have prevented the visual stimulus to directly affect primary somatosensory cortex activity. Interestingly, in Experiment 2 we fully replicate the magnification of somatosensory evoked activity induced by implicit visual bodily-self recognition, but an earlier latency that is more compatible with the activity of primary areas (around 45 ms).

Furthermore, we convincingly confirmed that self-hand recognition operates by modulating sensory activity within somatosensory areas when we next analyzed electrophysiological activity elicited by the second stimulus in Experiment 1. Indeed, we found that the somatosensory evoked activity in response to the second stimulus was significantly greater in pairs of different as compared to pairs of identical stimuli, but only in the With Self scenario. This effect suggests that the recognition of the self-hand triggered a sort of somatosensory change detection, by modulating tactile processing based on whether vS2 was preceded by an identical or different vS1. Interestingly, when analyzing visual evoked activity triggered by vS2, we replicated previous findings described in Chapter 1 that indicated that self-hand recognition enhanced visual change detection (Galigani et al., 2021). We observed greater electrophysiological activity when vS2 was different than identical to vS1 in the With Self scenario, whereas in the Without Self scenario such difference emerged only at a later latency.

To summarize, our electrophysiological results clearly demonstrate the involvement of tactile information in self-hand recognition, as reveals the specific modulation of somatosensory evoked activity by the visual presentation of the self-hand. This finding is fully consistent with the idea that bodily visual stimuli affect somatosensory processing, and in particular with pioneering studies showing that the vision of the body boosts tactile acuity relative to viewing a neutral object (Cardini et al., 2012; Haggard et al., 2003; Serino & Haggard, 2010). However, the specificity observed in our data for self-hand recognition indicates that the bodily self has a systematic influence on the somatosensory system. Differently from images depicting others' bodies, which cannot be felt, visual stimuli representing the bodily-self may have a preferential access to somatosensory information and it is in line with this view that the nervous system relies on the integration between visual features and sensory information to recognize the bodily self (Ferri et al., 2012a; Limanowski & Blankenburg, 2015; Myers & Sowden, 2008). Therefore, the present results provide substantial evidence in favor of an integrated, multisensory network devoted to the recognition of the bodily-self, where somatosensory cortex may constitute a crucial hub, and suggest that touch, and not vision, is the privileged sensory system devoted to self-hand recognition. In a future study, which is definition and is not part of this thesis, we would like to confirm the role of primary somatosensory area in self-hand recognition by inhibiting its activity with brain stimulation techniques. Indeed, we plan to interfere with the activity of the somatosensory area during an implicit self-hand recognition task to investigate how the loss of access to the somatosensory information of the hand affects self-other hand discrimination.

In Chapter 3, we further test the hypothesis of the role of a multimodal network in subserving bodily-self recognition by capitalizing on brain-damaged patients that show a disconnection within the fronto-parietal network.

2.5 References

Apps, M. A. J., & Tsakiris, M. (2014). The free-energy self: A predictive coding account of self-recognition. Neuroscience and Biobehavioral Reviews, 41, 85–97. https://doi.org/10.1016/j.neubiorev.2013.01.029

Arslanova, I., Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2019). Searching for bodies: ERP evidence for independent somatosensory processing during visual search for body-related information. NeuroImage, 195(March), 140–149. https://doi.org/10.1016/j.neuroimage.2019.03.037

Botvinick, M., & Cohen, J. D. (1998). Rubber hand ‘feels’ what eyes see. Nature, 391(February), 756.

Bruno, V., Ronga, I., Fossataro, C., Capozzi, F., & Garbarini, F. (2019). Suppressing movements with phantom limbs and existing limbs evokes comparable electrophysiological inhibitory responses. Cortex, 117, 64–76. https://doi.org/10.1016/j.cortex.2019.02.024

Cardini, F., Costantini, M., Galati, G., Romani, G. L., Làdavas, E., & Serino, A. (2011). Viewing one’s own face being touched modulates tactile perception: An fMRI study. Journal of Cognitive Neuroscience, 23(3), 503–513. https://doi.org/10.1162/jocn.2010.21484

Cardini, F., Longo, M. R., Driver, J., & Haggard, P. (2012). Rapid enhancement of touch from non-informative vision of the hand. Neuropsychologia, 50(8), 1954–1960. https://doi.org/10.1016/j.neuropsychologia.2012.04.020

Conson, M., Mazzarella, E., Esposito, D., Grossi, D., Marino, N., Massagli, A., & Frolli, A. (2015). “Put Myself Into Your Place”: Embodied Simulation and Perspective Taking in Autism Spectrum Disorders. Autism Research, 8(4), 454–466. https://doi.org/10.1002/aur.1460

Conson, M., Volpicella, F., De Bellis, F., Orefice, A., & Trojano, L. (2017). “Like the palm of my hands”: Motor imagery enhances implicit and explicit visual recognition of one’s own hands. Acta Psychologica, 180(September), 98–104. https://doi.org/10.1016/j.actpsy.2017.09.006

De Bellis, F., Trojano, L., Errico, D., Grossi, D., & Conson, M. (2017). Whose hand is this? Differential responses of right and left extrastriate body areas to visual images of self and others’ hands. Cognitive, Affective and Behavioral Neuroscience, 17(4), 826–837. https://doi.org/10.3758/s13415-017-0514-z

della Gatta, F., Garbarini, F., Puglisi, G., Leonetti, A., Berti, A., & Borroni, P. (2016). Decreased motor cortex excitability mirrors own hand disembodiment during the rubber hand illusion. ELife, 5(OCTOBER2016), 1–14. https://doi.org/10.7554/eLife.14972

Errante, A., Pia, L., Pinardi, C., Fogassi, L., & Garbarini, F. (n.d.). Anatomical connections associated with the pathological embodiment of other’s body parts: a probabilistic DTI tractography study.

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., & Garbarini, F. (2022). Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Communications, 4(1), 1–15. https://doi.org/10.1093/braincomms/fcac032

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A sensorimotor network for the bodily self. Journal of Cognitive Neuroscience, 24(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Fossataro, C., Bruno, V., Giurgola, S., Bolognini, N., & Garbarini, F. (2018). Losing my hand. Body ownership attenuation after virtual lesion of the primary motor cortex. European Journal of Neuroscience, 48(6), 2272–2287. https://doi.org/10.1111/ejn.14116

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. Journal of Cognitive Neuroscience, 20(8), 1507–1516. https://doi.org/10.1162/jocn.2008.20067

Frassinetti, F., Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., Avanzi, S., & Farnè, A. (2009). Visual processing of moving and static self body-parts. Neuropsychologia, 47(8–9), 1988–1993. https://doi.org/10.1016/j.neuropsychologia.2009.03.012

Galigani, M., Ronga, I., Fossataro, C., Bruno, V., Castellani, N., Sebastiano, A. R., Forster, B., & Garbarini, F. (2021). Like the back of my hand: Visual ERPs reveal a specific change detection mechanism for the bodily self. Cortex, 4. https://doi.org/10.1016/j.cortex.2020.10.014

Galvez-Pol, A., Calvo-Merino, B., Capilla, A., & Forster, B. (2018). Persistent recruitment of somatosensory cortex during active maintenance of hand images in working memory. NeuroImage, 174(February), 153–163. https://doi.org/10.1016/j.neuroimage.2018.03.024

Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2020). Revealing the body in the brain: An ERP method to examine sensorimotor activity during visual perception of body-related information. Cortex, 125, 332–344. https://doi.org/10.1016/j.cortex.2020.01.017

Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. Current Biology : CB, 13(5), 170–173. https://doi.org/10.1016/s0960-9822(03)00115-5

Harris, A. M., Dux, P. E., & Mattingley, J. B. (2018). Detecting unattended stimuli depends on the phase of prestimulus neural oscillations. Journal of Neuroscience, 38(12), 3092–3101. https://doi.org/10.1523/JNEUROSCI.3006-17.2018

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. Human Brain Mapping, 36(6), 2284–2304. https://doi.org/10.1002/hbm.22770

Longo, M. R., Schüür, F., Kammers, M. P. M., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. Acta Psychologica, 132(2), 166–172. https://doi.org/10.1016/j.actpsy.2009.02.003

Mouraux, A., & Iannetti, G. D. (2008). Across-trial averaging of event-related EEG responses and beyond. Magnetic Resonance Imaging, 26(7), 1041–1054. https://doi.org/10.1016/j.mri.2008.01.011

Musacchia, G., & Schroeder, C. E. (2009). Neuronal mechanisms, response dynamics and perceptual functions of multisensory interactions in auditory cortex. Hearing Research, 258(1–2), 72–79. https://doi.org/10.1016/j.heares.2009.06.018

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. NeuroImage, 42(4), 1669–1677. https://doi.org/10.1016/j.neuroimage.2008.05.045

Novembre, G., Pawar, V. M., Bufacchi, R. J., Kilintari, M., Srinivasan, M., Rothwell, J. C., Haggard, P., & Iannetti, G. D. (2018). Saliency detection as a reactive process: Unexpected sensory events evoke corticomuscular coupling. Journal of Neuroscience, 38(9), 2385–2397. https://doi.org/10.1523/JNEUROSCI.2474-17.2017

Ronga, I., Sarasso, P., Fossataro, C., Salatino, A., Garbarini, F., Ricci, R., & Neppi-Modona, M. (2018). Everything is illuminated: Prismatic adaptation lowers visual detection threshold in normal subjects. Journal of Experimental Psychology: Human Perception and Performance, 44(10), 1619–1628. https://doi.org/10.1037/xhp0000559

Ronga, I., Valentini, E., Mouraux, A., & Iannetti, G. D. (2013). Novelty is not enough: Laser-evoked potentials are determined by stimulus saliency, not absolute novelty. Journal of Neurophysiology, 109(3), 692–701. https://doi.org/10.1152/jn.00464.2012

Sarasso, P., Ninghetto, M., Salatino, A., Ronga, I., Bongiardina, A., Iarrobino, I., Neppi-Modona, M., & Ricci, R. (2019). Everything is (still) illuminated: Dual right cathodal-left anodal tDCS of PPC prevents fatigue on a visual detection task. Brain Stimulation, 12(1), 187–189. https://doi.org/10.1016/j.brs.2018.09.017

Sarasso, P., Ronga, I., Kobau, P., Bosso, T., Artusio, I., Ricci, R., & Neppi-Modona, M. (2020). Beauty in mind: Aesthetic appreciation correlates with perceptual facilitation and attentional amplification. Neuropsychologia, 136(November 2019), 107282. https://doi.org/10.1016/j.neuropsychologia.2019.107282

Sel, A., Forster, B., & Calvo-Merino, B. (2014). The emotional homunculus: ERP evidence for independent somatosensory responses during facial emotional processing. Journal of Neuroscience, 34(9), 3263–3267. https://doi.org/10.1523/JNEUROSCI.0106-13.2014

Serino, A., & Haggard, P. (2010). Touch and the body. Neuroscience and Biobehavioral Reviews, 34(2), 224–236. https://doi.org/10.1016/j.neubiorev.2009.04.004

Sugiura, M., Miyauchi, C. M., Kotozaki, Y., Akimoto, Y., Nozawa, T., Yomogida, Y., Hanawa, S., Yamamoto, Y., Sakuma, A., Nakagawa, S., & Kawashima, R. (2015). Neural mechanism for mirrored self-face recognition. Cerebral Cortex, 25(9), 2806–2814. https://doi.org/10.1093/cercor/bhu077

Vuilleumier, P. H., Arguissain, F. G., Alberto, J., Manresa, B., Neziri, A. Y., Nirkko, A. C., Andersen, O. K., Arendt-, L., & Curatolo, M. (2017). Psychophysical and electrophysiological evidence for enhanced pain facilitation and unaltered pain inhibition in acute low back pain patients. Journal of Pain, 18(11), 1313–1323. https://doi.org/10.1016/j.jpain.2017.05.008

Zeller, D., Friston, K. J., & Classen, J. (2016). Dynamic causal modeling of touch-evoked potentials in the rubber hand illusion. NeuroImage, 138, 266–273. https://doi.org/10.1016/j.neuroimage.2016.05.065

Chapter 3. Bodily self-recognition in patients with pathological embodiment

[This research has been published in Candini M, Fossataro C, Pia L, Vezzadini G., Gindri P., Galigani M., Berti A., Frassinetti F., Garbarini F. (2020). Bodily self-recognition in patients with pathological embodiment. Journal of Neuroscience Research. https://doi.org/10.1002/jnr.25109]

3.1 Introduction

In Chapter 1 we highlighted an implicit marker of the advantage in recognizing self-body parts, whereas in Chapter 2 we demonstrated that the somatosensory cortex plays a crucial role in bodily-self recognition. In this Chapter we aimed at corroborating the idea of the contribution of visual-sensorimotor associations in self-hand recognition, by capitalizing on brain-damaged patients affected by pathological embodiment.

Typically, in healthy participants the distinction between my body and other's body is automatic and immediate. However, evidence coming from experimental manipulation in healthy participants and in pathological populations indicate that our feeling of body ownership is a complex and multifaceted process with different brain mechanisms possibly serving different body representations. In healthy participants, for example, manipulating the integration of multisensory signals may induce the illusory feeling that a fake and external body-part is one's own. Growing neuroimaging and behavioral evidence on healthy participants revealed the mechanisms underlying this experience. During the rubber hand illusion (RHI; Botvinick & Cohen, 1998; Bucchioni et al., 2016; Burin et al., 2017; della Gatta et al., 2016; Tsakiris, Hesse, Boy, Haggard, & Fink, 2007; Zeller, Gross, Bartsch, Johansen-Berg & Classen, 2011; Zeller, Friston, & Classen, 2016), the enfacement illusion (D'Angelo et al., 2020; Sforza et al., 2010; Tsakiris, 2008), and the full-body illusion (D'Angelo et al., 2017, 2019; Ehrsson, 2007; Lenggenhager et al., 2007; Petkova & Ehrsson, 2008), participants identify themselves with another person's body part or with a virtual body. For instance, the classic RHI is elicited by simultaneously stroking the rubber hand and the participants' hand. After a short period of stimulation, participants start to experience the rubber hand as part of their own body. Interestingly, RHI may also affect self-hand recognition processes. Indeed, Longo and collaborators (2008) found that the incorporation of the rubber hand into the body image did affect the similarity that participants perceived between their own hand and the rubber hand. Participants who had experienced the RHI perceived their hand and the rubber hand as significantly more similar than participants who had not experienced the illusion. In a complementary experiment, it has also been shown that participants that are able to visually recognize their own hand in an image are less susceptible to the RHI illusion, thus supporting the link between the visual representation of the own body and the plasticity of the body representation (O’Dowd & Newell, 2020).

Critically, further interesting findings elucidating the grounds of the sense of body-ownership came from neurological and neuropsychological studies. One first example is provided by studies on somatoparaphrenic patients, who, after a right unilateral brain damage, show delusional beliefs about the contralesional side of their body. Crucially, these patients attribute their paralyzed limb to another person, exhibiting a sense of disownership for the affected body-parts (for a review see Garbarini, Fossataro, Pia, & Berti, 2020; Romano & Maravita, 2019; Vallar & Ronchi, 2009).

Recently, Garbarini and coworkers (Errante et al., 2022; Fossataro et al., 2016; Fossataro, Bruno, Gindri, et al., 2018; Fossataro et al., 2020; Garbarini et al., 2013, 2014, 2015; Garbarini & Pia, 2013; Pia et al., 2013, 2016, 2020; Ronga et al., 2019; Rossi Sebastiano, Poles, et al., 2022) described also the opposite behavior in brain-damaged patients who erroneously identify other people’s hand as their own. The term of *pathological embodiment* (PE) has been coined by the authors to refer to this clinical manifestation. Patients who are affected by PE are classified as E+ patients, while E- patients are subjects without PE. In this condition, the delusion of ownership spontaneously occurs when the examiner’s hand (hereinafter alien hand) is positioned on the table internally to the patient’s contralesional hand and according to the patient’s egocentric coordinates. Whenever the examiner’s hand is placed in this body-congruent position, E+ patients misattribute the alien hand to themselves and they treat and care for it as if it was their own hand. Interestingly, in the absence of the alien limb, E+ patients do not explicitly deny that their contralesional limb belong to themselves (as in somatoparaphrenic delusion, for a review see Gandola et al., 2012; Romano & Maravita, 2019; Vallar & Ronchi, 2009). Furthermore, PE does not occur when the alien hand is misaligned with the patient's shoulder, when it is perceived in allocentric perspective or positioned in the intact ipsilesional body-side and when, instead of a human hand, a rubber hand is used (Fossataro, Bruno, Gindri, et al., 2018; Garbarini et al., 2015; Pia et al., 2020). Going further, it has been revealed that, in E+ patients, the profound alteration of their corporeal representation affects both motor and somatosensory processing thus suggesting that this delusion is not a mere verbal confabulation, but instead, it reflects a real embodiment of the alien arm within the patient's sensorimotor system. Firstly, the alien hand movements modulate the motor parameter of the patient's intact arm movements (Garbarini et al., 2013) and the representation of the patient's personal/peripersonal space (Fossataro et al., 2016; Garbarini et al., 2015; Ronga et al., 2019), as if the moving alien hand was the patients' real hand. Secondly, somatosensory stimuli delivered to the alien hand elicit a comparable phenomenological/physiological response as those delivered to the own healthy hand (Garbarini et al., 2014; Pia et al., 2013).

Together, these studies suggest that the corporeal self-representation does not inevitably match the physical body, opening up a window to the understanding of how the sense of body ownership is constructed (Brugger & Lenggenhager, 2014). For instance, during the embodiment evaluation (see details in *Materials and methods section*) it is surprising how E+ patients seem to completely ignore the perceptive visual details (i.e., skin color, shape, age or dimension) coming from the alien hand, when it is placed in the contralesional (affected) body side, next to the patients' hand. Thus, even if both hands are visible on the table, patients do not use visual information to discriminate between the one's own and the alien hand. It is important to note that E+ patients cannot rely on one of the most important information that we use to identify our own body, i.e., proprioception, including both statesthesia (i.e., static position sense) and kinanesthesia (i.e., dynamic position sense). Indeed, so far, no E+ patients with spared position sense have been described (Pia et al., 2020). Importantly, in patients without pathological embodiment (E-), when the position sense is lost, the ability to visually discriminate between self and others' body is still present and they can rely on a normal elaboration of visual input to identify their own hand. On the contrary, in E+ patients, the ownership judgment seems to be based only on an abstract knowledge of body structure, so that, in the clinical evaluation, each stimulus matching the constraints of this aprioristic body spatial representation (e.g., a human hand aligned with the shoulder and perceived in egocentric perspective), regardless of its visual details, is felt as part of the own body.

Capitalizing on these clinical characteristics, in the present study we designed two experimental protocols to explore the bodily self visual recognition, by means of implicit and explicit judgments, that were submitted to a group of RBD patients, divided in two subgroups (E+ and E-), whose neuropsychological assessment and lesion mapping were provided. As discussed in the previous Chapters, It has been recently suggested that humans have, beyond an explicit recognition of their body, also an implicit knowledge of their own body-parts. Frassinetti and coworkers (2008; 2009; 2011; 2012) demonstrated that participants' performance is more efficient with self rather than other's body-parts (self-advantage effect). Intriguingly, this effect was not found when participants were explicitly required to judge if the lower or the upper stimulus corresponded to their own body-parts (Frassinetti et al., 2011). This dissociation suggests that implicit and explicit bodily self-recognition are based on different mechanisms or referred to different representations. Supporting this evidence, studies in neurological patients, reporting a lack of self-advantage effect in right but not in left brain-damaged patients (Frassinetti et al., 2008, 2009, 2010), revealed two distinct networks within the right hemisphere involved in visual processing of self-body stimuli.

Notably, none of these studies have considered the possible presence of PE and the distinction between E+ and E- RBD patients. Thus, the aim of the current study is to verify whether the impairment found in RBD patients in implicit/explicit self body-parts recognition is modulated by the presence of PE and investigate the role of visuo-sensorimotor network in bodily-self recognition.

3.2 Methods and Materials

3.2.1 Participants and neuropsychological assessment

Twenty-four healthy participants (11 males, mean age ± sd = 66.4 ± 10.3 years; mean education ± sd = 9.4 ± 4.4 years; hereinafter **Control group**), twenty RBD patients without pathological embodiment (9 males, mean age ± sd = 65.5 ± 8.4 years; mean education ± sd = 10.3 ± 4.3 years; hereinafter **E- group**) and twenty RBD patients with pathological embodiment (11 males, mean age ± sd = 68.7 ± 9.6 years; mean education ± sd = 7.2 ± 3.1 years; hereinafter **E+ group**) participated in the study. To verify that the three groups were not significantly different for education [$F_{2,59}$ = 2.93; P = 0.061; η^2_p =.09] and age [$F_{2,59}$ = 0.57; P = 0.56; η^2_p =.02], two One-way ANOVAs were conducted.

All participants were right-handed by their own verbal report. Patients were recruited at the ICS Maugeri (Castel Goffredo, Italy) and at the San Camillo Hospital (Torino, Italy).

To verify the presence of a general cognitive impairment the Mini-Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) or the Montreal Cognitive Assessment (MoCA; (Santangelo et al., 2015) was used. During the standard neurological evaluation, both primary motor and sensory deficits were assessed. Primary motor and sensory deficits were assessed during the standard neurological evolution whereby scores ranging from 0 (no deficit) to 3 (severe deficit) were assigned in accordance with the procedure validated in previous studies

(Bisiach et al., 1986; Pia et al., 2014; Ricci et al., 2016). Proprioception, as in a previous study (Fossataro, Bruno, Gindri, et al., 2018), was evaluated with two techniques for testing the limb localization: the Contralateral Limb Matching Task (CLMT) (Goble, 2010) and the Finger Localizing Test (FLT) (Hirayama et al., 1999). The presence/absence (+/-) of proprioceptive deficits in one of the two tests is indicated in Table 1. Based on previous studies (Fossataro et al., 2020; Pia et al., 2020), in which the presence of extra-personal neglect (N+ patients with extra-personal neglect; N- patients without extra-personal neglect) has been demonstrated to be more frequent in E+ than in E-, all patients were evaluated with the Bit Conventional scale (Halligan, Cockburn, & Wilson, 1991). E+ and E- patients did not differ for stroke onset (t_{38}=0.84; p=0.40). As regards the neurological/neuropsychological features, E+ and E- groups did not differ (Mann-Whitney U Tests, all p*s* > 0.3) in terms of general cognitive impairment (E-: 5%; E+: 10%), motor deficits (E-: 75%; E+: 75%), and personal neglect (E-: 25%; E+: 45%). Conversely, the two groups differed in terms of sensory deficit (E-: 60%; E+: 95%), proprioception (E-: 30%; E+: 100%), and extra-personal neglect (E-: 50%; E+: 90%), which were significantly (all p*s* < 0.04) more frequent in the E+ patients group than in the E- group. For details see Table 1.

All participants were naive to the purpose of the study and provided written informed consent before their participation. The study was approved by the local ethical committee (University of Bologna), and all procedures were in compliance with the Declaration of Helsinki (2013).

Patient	**Onset**	**Sex**	**Age**	**Aethiology**	**Cognitive Impairment**	**HP**	**HA**	**P**	**BIT-C**	**Personal Neglect**
E- 1	43	F	67	I	-	3	1	-	141	-
E- 2	50	F	79	I	-	3	3	+	141	-
E- 3	34	F	55	I	-	3	1	-	144	-
E- 4	65	M	57	I	-	3	3	-	119	+
E- 5	42	M	60	H	-	3	0	+	112	+
E- 6	34	M	63	I	-	3	0	-	145	-
E- 7	40	M	66	H	-	3	3	-	141	-
E- 8	38	F	68	I	-	3	3	+	142	-
E- 9	35	F	69	I	-	1	0	-	124	+
E- 10	75	F	57	I	-	0	0	-	129	-
E- 11	65	F	61	H	-	3	0	-	142	-
E- 12	148	M	72	I	-	3	3	-	113	+
E- 13	~~44~~	F	82	H	-	0	0	-	124	-
E- 14	80	M	76	I	-	0	0	-	129	-
E- 15	59	F	63	I	-	0	1	+	88	-
E- 16	92	M	74	H	-	3	3	-	97	+
E- 17	37	M	69	I	+	0	0	-	80	-
E- 18	198	F	56	I	-	3	3	+	109	-
E- 19	54	F	51	H	-	1	1	+	120	-
E- 20	35	M	65	I	-	3	1	-	135	-
E+ 1	60	M	62	I	-	0	1	+	64	-
E+ 2	70	M	70	I	-	2	0	+	68	-

E+ 3	70	F	70	I	-	3	3	+	51	+
E+ 4	87	M	45	H	-	3	3	+	86	-
E+ 5	26	M	73	H	-	3	3	+	66	-
E+ 6	80	M	56	H	-	3	3	+	111	+
E+ 7	75	F	77	H	-	3	3	+	30	+
E+ 8	60	F	74	I	-	3	3	+	85	+
E+ 9	69	F	74	I	+	0	3	+	100	-
E+ 10	30	F	62	I	-	3	3	+	57	-
E+ 11	36	M	85	I	-	3	3	+	57	-
E+ 12	48	F	75	I	-	3	1	+	69	-
E+ 13	69	F	75	I	-	3	3	+	14	+
E+ 14	63	M	58	H	-	3	3	+	20	-
E+ 15	42	F	79	I	-	0	1	+	93	+
E+ 16	34	M	75	I	-	3	3	+	125	-
E+ 17	49	M	57	H	-	3	1	+	122	+
E+ 18	20	M	65	I	-	0	1	+	133	-
E+ 19	26	F	74	H	+	3	1	+	143	-
E+ 20	78	M	68	I	-	0	1	+	16	+

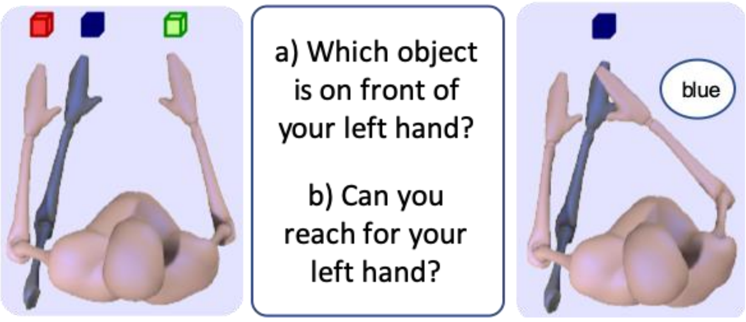
Table 1: Clinical and neuropsychological data of right brain damaged patients according to the pathological embodiment. E- = patients without pathological embodiment; E+ = patients with pathological embodiment; Onset= days between stroke onset and assessment; Sex (F = female; M= male); Aetiology (I = ischemic stroke; H = hemorrhagic stroke); Cognitive impairment indicated as present (+) or absent (-) (scores are corrected for years of education and age according to each battery (MMSE cut off > 24; MoCA cut off > 17); HP = motor deficit; HA = sensory deficit; P= Proprioceptive

deficit, indicated as present (+) or absent (-); BIT-C = score obtained at the Conventional Subscale (cut off > 129); Personal Neglect = score obtained at the Fluff test (cut off omissions ≤ 2), indicated as present (+) or absent (-).

Embodiment evaluation

At the beginning, all patients were assessed with an ad hoc protocol to evaluate the presence/absence of the pathological embodiment (Fossataro et al., 2016, 2020; Fossataro, Bruno, Gindri, et al., 2018; Garbarini et al., 2013, 2014, 2015; Pia et al., 2013).

Patients sat on a chair with both hands lying on the table. The experimenter positioned her hand (alien hand) on the table between the patient's body and the patient's affected hand. The alien hand was in a congruent position according to the patient's trunk midline and aligned with the patient's contralesional shoulder. To cover the patient and the experimenter's arms, leaving all the hands visible on the table, a sheet of tissue was adopted. Three colored objects were positioned on the table: the blue one in front of the examiner's hand, the red one in front of the patient's affected hand, and the green one in front of the patient's intact ipsilesional hand. Patients had to a) count how many objects and hands were on the table, b) perform movements with their intact hand in order to reach their contralesional affected hand and c) identify their affected hand on the basis of the colored object in front of it. To be included in the study, a patient has to be errorless in counting three objects and three hands on the table (i.e., we did not include patients who, due to a severe ecological neglect, counted only two objects and two hands and omitted the object and the hand more on the left). To be included in the E+ group, a patient has to fail both motor and verbal tasks, (i.e., to reach the alien hand instead of his/her own hand and to name the color of the objects in front of the alien hand instead of naming the color of the cube in front of his/her own hand) (see Figure 1). Thus, to be included in the E- group, a patient has to correctly perform both the motor and verbal tasks.



a) Which object is on front of your left hand?

b) Can you reach for your left hand?

Figure 10. Embodiment evaluation The patient had to identify his/her left hand by naming the colored objects in front of it and by reaching his/her left affected hand with the right intact hand. The alien hand, belonging to the confederate, was aligned with the patient's left shoulder.

3.2.2 Stimuli and procedure of hand recognition task

Grey-scale pictures of the dorsal view of right and left hands were adopted as stimuli. In a session prior to the experiments, participants' hands were photographed according to the experimental procedure previously described (Frassinetti et al., 2011). Stimuli depicted the participant's own left or right hand ('self' trials) in half of the trials (n=32). In the other half of the trials, stimuli depicted the right or left hand of other three individuals (n=32; 'other' trials). The 'other' trials consisted of three stimuli selected from a database of hands pictures as the best match with each participant's hand for size, age, skin color and sex to make the task more difficult. Since in the clinical assessment the PE selectively occurs when the alien hand is placed in an egocentric perspective, we aimed at verifying possible differences between E+ and E- patients in bodily self recognition driven by the visual perspective of hand. Thus, each stimulus was presented both in egocentric and allocentric perspective.

Participants sat in front of a PC screen, at a distance of about 50 cm. At the beginning of each trial, a central fixation cross lasting 1000 ms was displayed, followed by the hands' pictures on a white background. E-Prime 2.0 was adopted for stimuli presentation (Psychology Software Tools Inc.) and each trial ended as soon as the participant verbally responded. In Experiment 1 (implicit task), for each trial three stimuli were simultaneously presented, vertically aligned on the PC screen. The central stimulus (target) was presented in a black frame. Participants were instructed to judge whether the lower or the upper hand corresponded to the central target. In Experiment 2 (explicit task), each trial consisted of two hand pictures, one in the upper and the other in the lower part of the screen, while the central black frame was empty. Participants were required to explicitly judge whether one of the two displayed hands corresponded or not to their own hand (see Figure 11). Participants were asked to verbally respond as accurately as possible, and the experimenter manually recorded the participants' response by using one of the three assigned keys on the keyboard. Because of the nature of the stimuli, which depicted a participant's body-part, we opted for a vocal instead of a manual response, which could have biased the results.

Thus, each experiment comprised a total of 64 trials and consisted of four conditions: self-right hand, self-left hand, other-right hand, other-left hand. In each condition, 16 trials were presented: in half of the trials, stimuli were presented in egocentric perspective, whereas in the other half stimuli were presented in allocentric perspective. Since Experiment 1 investigated the implicit and Experiment 2 the explicit bodily self-recognition, Experiment 1 was always conducted before Experiment 2. Each participant performed both experiments in one single session which lasted one hour.

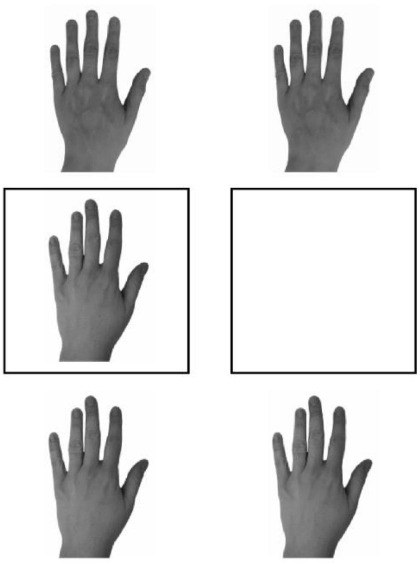


Figure 11. Experimental stimuli. An example of a single trial for the Implicit task (on the left) and the Explicit task (on the right).

3.2.3 Control experiment on object visual recognition

The same procedure was adopted as in the implicit bodily self-recognition task, except that stimulus was grey-scale picture of object, instead of body-part. The task consisted of a total of 32 trials in which guitar (n = 16) or scissor (n = 16) were presented in egocentric and allocentric perspective (see Figure 12). For each trial, three stimuli were simultaneously presented until the participant’s response. The central stimulus (target) was presented in a black frame. Participants were required to judge whether the lower or the upper stimulus corresponded to the central one. Stimuli presentation was controlled by E-Prime 2.0 (Psychology Software Tools Inc.) and each trial was timed-out by the participant’s vocal response.

Figure 12. Stimuli of the control experiment. An example of a single trial for the control experiment.

3.2.4 Statistical analyses

We performed a statistical power analysis to estimate the sample size based our previous study (Candini et al., 2016). The a priori estimated sample size was N = 60 (20 for each group) with a power=0.95 and an effect size *f* = 0.19 (GPower 3.1.9).

We separately analyzed data from Experiment 1 (Implicit task) and Experiment 2 (Explicit task) by using STATISTICA 10 (StatSoft Europe). According with the definition adopted in a previous study (Frassinetti et al., 2008), we compared trials in which one of the stimulus belonged to the participant (Self condition) and trials in which no pictures belonged to the participant (Other condition).

To compare healthy participants and patients' performance two ANOVAs, separately for Implicit and Explicit task, were conducted on accuracy with Group (Controls, E+ and E- patients) and Sex (Male and Female) as between-subjects factor and Owner (Self and Other), Laterality (Left and Right hand) and Perspective (Egocentric and Allocentric) as within-subject factors.

In order to look in more details at the nature of errors made by participants in the explicit recognition of self body-parts, the percentage of False Alarms (FA; erroneous recognition of self-hand calculated in Other trials), and the percentage of Misses (erroneous rejection of self-hand calculated in Self trials) were compared across the three groups. Two one-way ANOVAs were separately conducted on percentage of FA and MISS errors with Group (Controls, E- and E+ patients) as between-subject factor.

Further analyses were conducted on neurological/neuropsychological tests in which a significant difference between E+ and E- was found (see details in section 2.1 *Participants and neuropsychological assessment).* Two Analyses of Covariance (ANCOVA), separately for Implicit and Explicit task, were performed on accuracy with Group (E- and E+ patients) as between-subjects factor and scores obtained at test assessing the presence of hemianesthesia (HA) and neglect (BIT-C) scales as covariate. Since an impairment in proprioception was present in all E+ patients, a comparison between E- patients with and without proprioceptive deficit was conducted by using a t-test. Finally, a correlation analyses were conducted on BIT-C score and HA and the percentage of accuracy in E+ and E- patients, separately for Implicit and Explicit tasks. The Duncan test was adopted to conduct post-hoc analyses. The Partial eta square (η^2_p) express the magnitude of effect size.

3.2.5 Lesion mapping and analysis

Brain lesions were identified by means of Computed Tomography and Magnetic Resonance digitalized images (CT/MRI) of 18 E+ patients and 14 E- patients (8 out of 40 CT/MRI are missing). For each patient, the location and extent of brain damage was delineated and manually mapped in the MNI stereotactic space by using MRIcro software (Rorden & Brett, 2000). First, to approximate the slice plane of the patient's scan, the MNI template was rotated (pitch only). Second, brain lesions were manually drawn onto each correspondent template slice by using anatomically landmarks (MC and CF), drawn the lesion. Then, drawn lesions were inspected by two trained raters (FF and LP) and, in case of disagreement, an intersection lesion map was used. Finally, each lesions map was rotated back into the standard space applying the inverse of the transformation parameters used in the stage of adaptation to the brain scan.

The lesion overlay percentage maps for the E+ and E- patients were calculated from all lesions and superimposed on a ch2 template using MRICron. Then, we performed a subtraction analysis between E+ and E- patients' lesions, and the region more frequently damaged in E+ patients with respect to E- patients was extracted. Since MRI/CT scans of 8 out of 40 patients are missing, we compared 18 E+ vs 14 E-. Note that, in this sample of 32 patients, the presence of somatosensory deficits is equally distributed between groups, while the presence of neglect is greater in E+ than in E- patients (as in the full sample). To control for this aspect, we performed an additional subtraction analysis in a subsample of 23 patients (16 N+E+ and 7 N+E-). Furthermore, to control for the lesion volume, we extracted the voxels lesioned in each patient and we entered them in an unpaired t-test (2-tailed).

Finally, lesion-symptom correlation employing a standard voxel-based approach based on lesion overlay [i.e., the voxel-based lesion-symptom mapping (VLSM, Rorden, Karnath, & Bonilha, 2007)] were computed to examine the more frequently lesions associated with PE using the embodiment assessment as predictor. VLSM were implemented using the non-parametric mapping (NPM; Rorden et al., 2007), which allows to compare the presence or absence of a lesion in a given cortical area on a voxel-by-voxel basis between the two groups by computing independent group t-tests (Liebermeister test). Furthermore, we also performed a second VLSM to examine the more frequently lesions associated with the tendency of hyper attributing the other hand to themselves (i.e., committing false alarm errors) by including false alarms as predictor also controlling for the lesion extension. In both analyses permutation thresholding with 1000 iterations was used to apply corrections for multiple comparisons (using family-wise error) in the whole-brain analyses. Quantitative estimates of grey and white matter regions involvement were obtained by superimposing the AAL anatomical template (Tzourio-Mazoyer et al., 2002) and the JHU-white matter template (Hua et al., 2008).

3.3 Results

3.3.1 Experiment 1: Implicit task

A significant effect for the variable **Group** ($F_{2,58}$=17.86; P=0.001; η^2_p=0.38) and its interaction **Laterality x Owner x Group** ($F_{2,58}$=5.15, P=0.009; η^2_p=0.15) was found. Considering the *within-group* differences, for the right hand, a self-advantage effect emerged only in the control group (self = 93% vs. other = 87%, p=0.047), whereas both in E- (79% vs. 78%) and E+ patients (63% vs. 68%) no significant within-group differences were observed (p>0.09 for all comparisons). For the left hand, no significant difference between self and other's hand was found in all groups (p>0.21 for all comparisons): Controls (90% vs. 93%), E- patients (89% vs. 87%)[1] and E+ patients (69% vs. 68%).

Interestingly, concerning the *between-groups* differences, E- patients performed selectively worse than Controls only when the stimulus depicted the right one's own hand (E-=79% vs. C=95%; P=0.041), whereas E+ patients performed worse than Controls in all conditions (all p*s*<0.008). Finally, E+ patients were overall less accurate than E- patients (all p*s*<0.05), with the exception of the right other hand (P=0.176; see Figure 13). The factor Sex was not significant [$F_{1,54}$=0.51, P=0.48] as well as the interaction with other factors [all p*s*>0.07]. E- patients were less accurate with right than left hands (all ps < .002), regardless of the ownership of the stimuli.

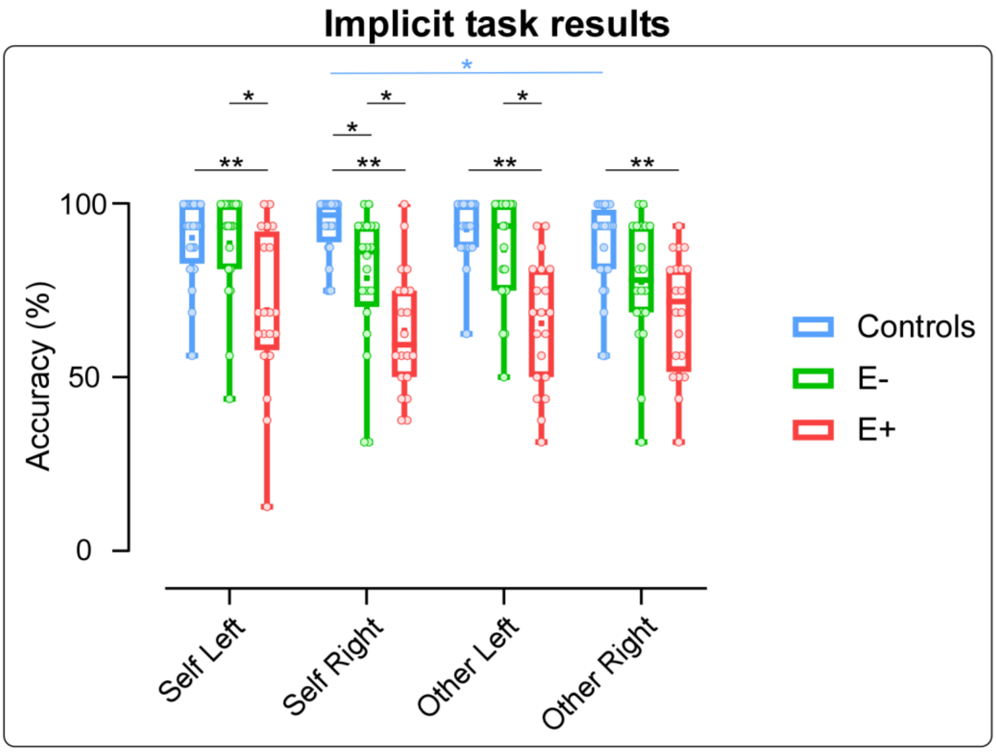


Figure 13. Implicit task. The Implicit task's accuracy percentages are displayed as a function of Ownership (Self, Other) and Laterality (Left, Right) respectively for Controls (in light blue), E- (in green) and E+ (in red) patients. In the boxplots, the whiskers represent the minimum and the maximum value, the limits of the box represent the first and the third quartile, the median is depicted by the line that divides the box into two parts, and the cross represents the mean. Dots represents individual values. Asterisk indicates a significant comparison (*P<0.05; **P<0.005; ***P<0.0005).

3.3.2 Control experiment on object visual recognition

Previous analyses showed that E+ patients were generally impaired in all conditions considered. However, to exclude that the observed results might be ascribed to a more general impairment in matching visual stimuli, we perform a control experiment in which objects (guitars and scissors) were adopted as stimuli. If the deficit observed in E+ selectively emerged for body, we expected a worse performance when body and objects were compared. By contrast, a lack of significant difference between body and objects may suggest a general impairment in matching visual stimuli.

In this experiment, we compared the performance of each single patient of a subgroup of eight patients (four E+ and four E- patients) with a subgroup of seventeen controls.

The difference in percentage of accuracy between the body visual matching recognition task and the object visual matching recognition task was tested by comparing the performance of each single case with that one of the control group. To this aim, we applied the function offered in Matlab (https://www.mathworks.com/matlabcentral/fileexchange/62968-crawford-howell-s-modified-t-test-and-revised-standardized-difference-test-rsdt) for Crawford and Garthwaite's (2007) Standardized Difference Test. This test is specifically devised to test differential deficits in a single case on two different tasks (Crawford & Garthwaite, 2007).

Crawford tests revealed a significant difference when the performance at the two tasks in each E+ patient was compared to the control group [E+1: $t_{(16)}=2.58$, $P=0.02$; E+2: $t_{(16)}=5.16$, $P<0.001$; E+3: $t_{(16)}=4.17$, $P<0.001$; E+4: $t_{(16)}=9.84$, $P<0.001$]. Whereas, when the performance at the two tasks in each E- patient was compared to the control group, no difference emerged in 3 out of four patients [E-1: $t_{(16)}=0.77$, $P=0.45$; E-2: $t_{(16)}=1.54$, $P=0.14$; E-3: $t_{(16)}=1.06$, $P=0.31$]. The performance at the two task in E-4 was instead significantly different compared to controls [E-4: $t_{(16)}=3.98$, $P=0.001$].

Indeed, the difference between body and object stimuli was significantly bigger for E+ patients (i.e., body worse than object) compared to controls. The E- patients showed the same pattern of controls except for one patient, who showed an opposite pattern (i.e., object worse than body; see Figure 14).

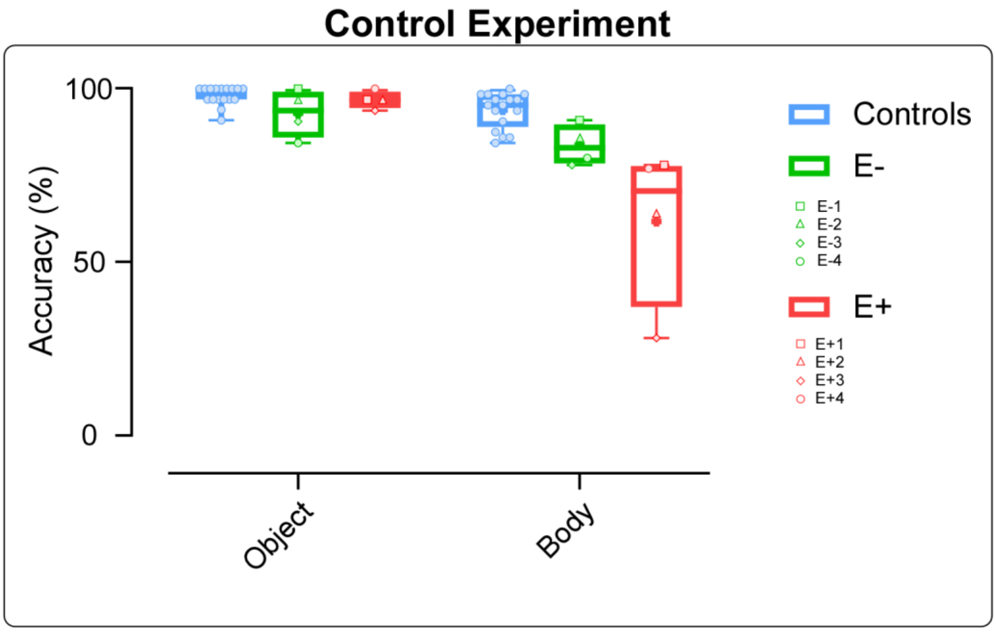


Figure 14. Control experiment results. The accuracy percentages in both Object and Body task are depicted for Controls (light blue), E- (green) and E+ patients (red), respectively. In the boxplots, the whiskers represent the minimum and the maximum value, the limits of the box represent the first and the third quartile, the median is depicted by the line that divides the box into two parts, and the cross represents the mean. Dots represents individual values. In E- and E+ patients groups each patient is represented with a different symbol.

3.3.3 Experiment 2: Explicit task

A significant effect for the variable **Group** [$F_{2,58}$=11.47, P=0.001; η^2_p=0.28] and the interaction **Owner x Group** [$F_{2,58}$=3.82, P=0.028; η^2_p=0.12] was found. Notably, the significant interaction was explained by the opposite pattern observed in E+ patients vs. E- patients and Controls. Indeed, considering within-group comparisons, E+ patients showed a greater accuracy for *Self* than *Other* stimuli (P=0.029), whereas both E- patients (P=0.161) and Controls performed worse with *Self* than *Other* stimuli (P=0.26), even if these comparisons failed to reach the significant level. When we looked at the between-group comparisons, with *Self’* stimuli, a worse performance, compared to Controls (51%), was observed in patients which reach the significant level in E- (34%; P=0.036) but not in E+ (39%, P=0.13). The difference between the last two groups was not significant (P=0.51). A completely different pattern of result emerged when *Other’* stimuli were considered: E+ patients (22%) performed significantly worse than Controls (60%, P=0.001) and E- patients (45%; P=0.003), whereas the last two groups were not significantly different (P=0.073; see Figure 15). Thus, the E+ patients’ performance was worse, as compared to E- patients and Controls, when they have to judge the *Other’* stimuli since they frequently attributed them to themselves. The factor Sex was not significant [$F_{1,58}$=1.46, P=0.233] as well as the interaction with other factors [all p*s*>0.085].

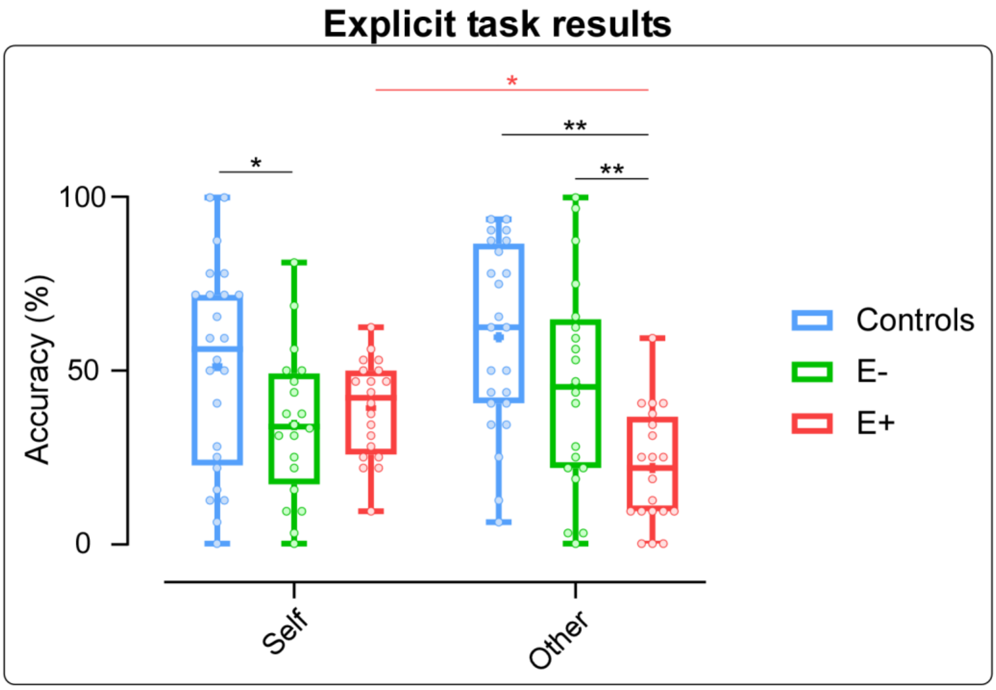


Figure 15. Explicit task. The Explicit task’ accuracy percentages are represented as a function of Ownership (Self, Other) respectively for Controls (light blue), E- (green) and E+ patients (red). In the boxplots, the whiskers represent the minimum and the maximum value, the limits of the box represent the first and the third quartile, the median is depicted by the line that divides the box into two parts, and

the cross represents the mean. Dots represents individual values. Asterisk indicates a significant comparison (*P<0.05; **P<0.005; ***P<0.0005).

Analysis on type of errors

The analysis conducted on FA errors revealed a significant main effect of **Group** [$F_{2,61}$=5.37, P=0.007, η^2_p=0.15]. Post-hoc comparisons revealed that E+ patients (78%) made higher False Alarms than E- patients (56%; P=0.002) and Controls (64%; P=0.04), whereas no differences between E- patients and Controls (P=0.22).

The analysis conducted on Misses failed to reveal a main effect of Group [$F_{2,61}$=0.27, P=0.77, η^2_p=0.01] suggesting that the three groups equally performed (E+ patients: 61% E- patients: 64%; Controls: 60%; P>0.60; Figure 16).

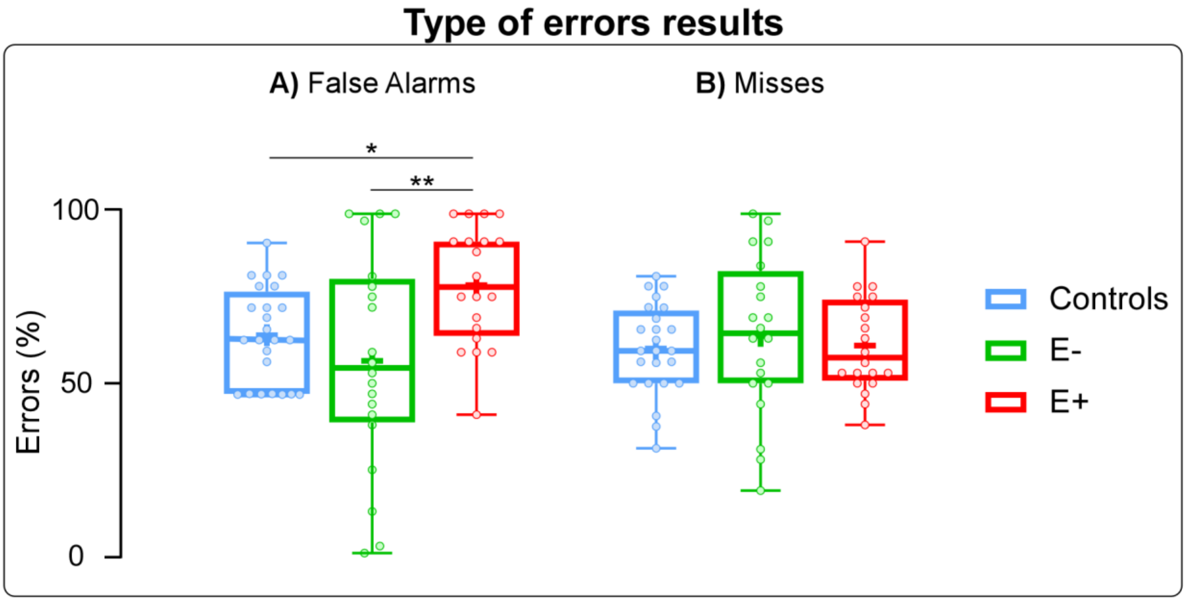


Figure 16. Type of errors results. Percentages of false alarms (A) and misses (B) are represented for Controls (light blue), E- (green) and E+ patients (red). In the boxplots, the whiskers represent the minimum and the maximum value, the limits of the box represent the first and the third quartile, the median is depicted by the line that divides the box into two parts, and the cross represents the mean. Dots represents individual values. Asterisk indicates a significant comparison (*P<0.05; **P<0.005; ***P<0.0005).

Finally, the sensitivity (d prime) and the type of criterion (beta) underlying patients' judgment were compared across the three groups by using two One-way ANOVAs. The analysis on sensitivity revealed a significant main effect of **Group** [$F_{2,61}$=5.74; P=0.005, η^2_p=0.16]: E+ patients (-1.32) were lower sensitive than E- patients (-0.74; P=0.009) and Controls (-0.65; P=0.004) in discriminate between the two stimuli. The analysis on the type of criterion failed to reveal a main effect of Group [$F_{2,61}$=3.01; P=0.06, η^2_p=0.09] suggesting that no difference emerged across the three groups for the criterion adopted in the explicit judgment (E+ patients: 4.04; E- patients: 3.14; Controls: 1.22).

3.3.3.1 Analysis to control for neurological and neuropsychological deficits

Implicit Task: Experiment 1

In ANCOVA analysis, no significant effect emerged for each considered covariate variable (all p*s*>0.38), or for its interaction with the variable Group. The variable Group was always still significant (all p*s*<0.05): E+ (67%) performed worse compared to E- patients (83%). T-test was not significant [t_{18}=0.27, P=0.79], excluding that proprioceptive deficit may influence the performance in implicit bodily self-recognition.

The Pearson's correlation on BIT-C score and percentage of accuracy was not significant either in E+ patients (r=-0.24, P=0.31) and E- patients (r=0.26, P=0.27). Similarly, the Pearson's correlation on hemianesthesia score and percentage of accuracy was not significant either in E+ patients (r=-0.28, P=0.24) and E- patients (r=0.24, P=0.32).

Explicit Task: Experiment 2

In ANCOVA no significant effect emerged for each considered covariate variable (all p*s*>0.23), or for its interaction with the variable Group. The variable Group was always still significant (all p*s* <0.05): E+ (31%) performed worse compared to E- patients (41%). Moreover, t-test was not significant [t_{18}=0.47, P=0.54], excluding that proprioceptive deficit may influence the performance in explicit bodily self-recognition.

The Pearson's correlation on BIT-C score and percentage of accuracy was not significant either in E+ patients (r=-0.06, P=0.81) and E- patients (r=0.33, P=0.15). The Pearson's correlation on hemianesthesia score and percentage of accuracy was not significant level either in E+ patients (r =-0.09, P=0.72) and E- patients (r =0.24, P=0.32).

3.3.3.2 Lesion mapping results

The area of maximal overlay across E+ patients is centered around the insula, external capsule, superior corona radiata, middle and superior temporal gyrus, rolandic operculum and the superior longitudinal fasciculus (SLF) (Figure 8a). Whereas in E- patients the area of maximal overlap is centered around the insula, external capsule, superior corona radiata, putamen and rolandic operculum (Figure 8b). The subtraction analysis shows that SLF and middle temporal gyrus were more frequently damaged in E+ patients as compared to E- patients group (Figure 8c). The additional subtraction analysis in the subsample of 23 patients confirms the greater involvement of SLF and middle temporal gyrus that were more frequently damaged in E+ patients as compared to E- patients group.

The T-test performed over the lesion volume showed that the two groups did not differ in terms of lesion volume (t_{30}= -1.09; P= 0.28), thus ruling out that any difference in the lesional pattern between group was due to differences in the lesion volume.

VLSM performed on the PE assessment showed that lesions involving voxels within middle temporal gyrus and SLF were significantly associated with the presence of PE (Figure 8d). The threshold for statistical significance was z=3.74030 (corrected, P<0.05) and the maximum voxels values were around the middle temporal gyrus (z= 3.74033, P<0.05) and SLF (z=

3.74030, P<0.05) that partially corresponds to the area of maximal overlay indicated on the percentage lesion overlay maps.

VLSM performed on the false alarm errors confirmed the obtained results, showing that lesions involving voxels within SLF was significantly associated with the tendency of committing false alarm errors (Figure 17). The threshold for statistical significance was z=-3.622 (corrected, P<0.05) and the maximum voxels values were within SLF (z=-3.935, P<0.02). The association of SLF to the tendency of hyper attributing the other hand to themselves was confirmed also controlling for the lesion extension.

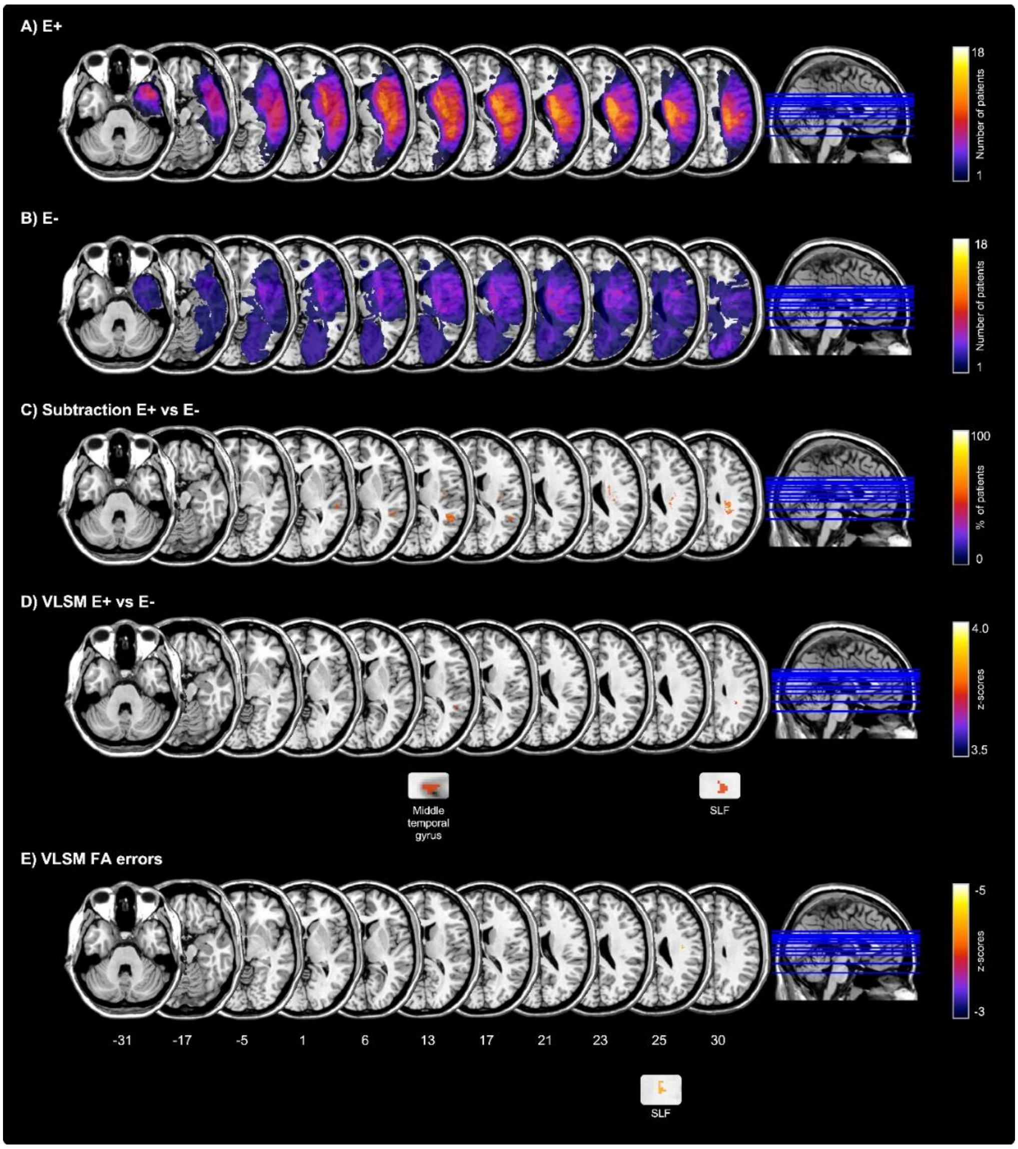


Figure 17. Overlay lesion plots. a) 18 E+ patients and b) 14 E- patients. The regional frequency of brain lesions in each area is expressed according to the color scale ranging from dark purple to light yellow. c) Subtraction lesion plot. The plot represents the region more frequently damaged in E+ group illustrated by different colors, from dark purple to light yellow. Only brain regions that were at least 50% or more frequently damaged in E+ with respect to E- patients are shown. d) VLSM E+ vs E- results. High z-scores (light yellow) indicate that lesions to these voxels have a highly significant association with PE. e) VLSM FA errors results. High z-scores (light yellow) indicate that lesions to these voxels have a highly significant association with the tendency of committing false alarm errors. Only voxels that were significant at P=0.05 (corrected with 1000 permutations) are shown. Axial slices are numbered according to MNI z coordinate.

3.4 Discussion

We commonly take for granted that "*our body may be the object that we know the best",* as Fréderique de Vignemont said (pp. 5, De Vignemont, 2018). However, following a brain damage, the ability to correctly recognize our body may be impaired, as suggested by several neuropsychological evidence (Moro et al., 2016; Candini et al., 2016; Frassinetti et al., 2008; for a review see, Garbarini et al., 2020; Romano & Maravita, 2019; Vallar & Ronchi, 2009).

The present study focused on the relationship between the sense of body ownership, selectively damaged in neuropsychological patients affected by pathological embodiment, and the implicit and explicit bodily self-recognition processing. In particular, as corroborated by lesional analysis described above, we also investigated the relationship between the impaired ability to recognize the own body and a lesioned anterior-posterior connectivity Thus, two groups of RBD patients, with (E+) and without (E-) pathological embodiment, were compared to a group of neurologically healthy participants adopting two experimental tasks developed for exploring implicit (Experiment 1) and explicit bodily self-recognition (Experiment 2), respectively.

In the ***Implicit Task***, when a matching to sample task was required without an explicit recognition of one's own hand, we observe differences both *within* and *across* the three groups. Regarding the differences *within* groups, in healthy participants a self-advantage (i.e., a more accurate performance for *Self* than *Other* stimuli) emerged when right hands were displayed. We acknowledge that in a previous study on bodily self recognition in which the same paradigm was adopted, no difference for stimuli depicting left and right hand was found (Frassinetti et al., 2008), however the occurrence of such a facilitation when judging one's own right compared to others' hands is in accord with recent findings in young right-handed healthy participants (Conson et al., 2010, 2017; Ferri et al., 2011; Frassinetti et al., 2011; Galigani et al., 2021). In right-handed participants, the neural efficiency of the sensorimotor network contralateral to the dominant (right) hand can be enhanced, thus explaining the observed facilitation for the right *Self* hand, at least in our sample. Indeed, it was demonstrated (Ferri et al., 2012a; Frassinetti et al., 2011) that the implicit visual recognition of one's own hand activates a sensorimotor experience-based representation of the hand. Importantly, this advantage in implicit self-body recognition was not present in both E- and E+ patients. The lack of this facilitation suggests that, following a right brain damage, the ability to implicitly recognize one's own body-parts is severely impaired. Present data confirm and extend previous neuropsychological findings (Frassinetti et al., 2008, 2009, 2010; but see also Candini et al., 2018 on self-voice recognition). First, in E- patients the self-advantage is lost (i.e., for the right hand, no difference between Self and Other stimuli was found), but their overall performance was comparable to that shown by healthy controls. Going further, E+ patients not only did not exhibit the self-advantage, but they also showed a lower overall performance with respect to both healthy controls and E- patients. Thus, at the Implicit task, the difference between E+ and E- patients is not specific for the Self stimuli, but it emerges in all experimental conditions. To exclude that the worst performance observed in E+ patients during the Implicit task was simply due to a general impairment when performing a visual discrimination task, we conducted a control experiment in which objects, instead of hands, were presented. We found that E+ patients (but not E- patients) performed worse with hands as compared to objects, suggesting that their impairment is specific for visual processing of body parts, at least when they include human hand images.

In the ***Explicit Task***, when bodily self-recognition was explicitly required, differences were found *across* the three groups: both E+ and E- showed an overall worse performance than Controls, confirming that a right brain lesion impairs the ability to explicitly discriminate between self and other's body (Candini et al., 2018, 2016). When we look at the *within* group comparisons no differences between Self and Other stimuli emerged, even if we observed a worse performance with Self than Other stimuli in both Controls and E- patients. This lack of significance can be explained by a difference in term of age (Frassinetti et al., 2011) and of experimental paradigm (Candini et al., 2018) with previous studies in which a "self-disadvantage effect" emerged (i.e., a worse performance with self than other stimuli).

More critical for the present study, while in E- patients, with intact body ownership, the same pattern shown by healthy controls was present, E+ patients performed worse with *Other* compared to *Self* stimuli. In this respect, it is worth to note that a bad performance with *Other* stimuli means the tendency to hyper attribute others' hand to themselves (i.e., higher false alarm rates when compared to E- patients; see Analysis of type of errors). This means that, at the explicit level, the same type of errors observed during the ecological evaluation, when PE is induced by the physical presence of the alien hand, emerges also when patients have to recognize hand images displayed on a computer screen, thus suggesting that explicit visual body recognition is a critical factor in PE. However, when hand pictures were displayed on a screen (as in the Explicit Task), instead of real hands positioned either on the right or on the left patients' body-side (as during the clinical evaluation), some important differences emerged.

In particular, we know from the literature that, when the alien limb was in the intact (right) body-side or when it was in allocentric perspective, E+ patients correctly recognized it as belonging to another person (Garbarini et al., 2013, 2014, 2015; Pia et al., 2013, 2020). On the contrary, in the Explicit Task, neither hand laterality nor perspective effects were found. This means that, in E+ patients, the explicit self-other body discrimination is damaged irrespective of the ecological constraints of the pathological embodiment that seems to be not relevant when stimuli are pictures displayed on a screen.

Importantly, even if tactile deficit and extra-personal neglect are more common in E+ patients, additional ANCOVAs further confirm that the worse performance of E+ patients, both in Implicit and Explicit tasks, cannot be ascribed to the greater frequency and severity of neurological and cognitive deficits. Indeed, when scores obtained at the tactile evaluation, as well as at the BIT-C battery, were considered as covariate variables, the difference between the two patients' groups was still present, excluding that the observed difference, both at implicit and explicit levels, were simply due to greater somatosensory or attentional and visuospatial impairments. These negative results were also confirmed by additional correlation analyses, showing no significant effects when scores at the tactile evaluation and at the BIT-C battery were used to predict the patients' performance at implicit and explicit tasks. In a similar vein, even if proprioceptive deficits are always associated to the pathological embodiment in our sample, their presence also in E- patients proves that the position sense loss is necessary but not sufficient for the pathological embodiment to occur (see Fossataro et al., 2020; Pia et al., 2020). This is also confirmed by *ad hoc* analyses showing no significant differences between E- patients with and without proprioceptive deficit. Thus, the phenomenon of pathological embodiment may be due to the co-occurrence of a proprioceptive deficit and an impaired recognition of the visual characteristics of the hand.

From an anatomical point of view, the present data (see Figure 8d) support the view of PE as a disconnection deficit with the Superior Longitudinal Fasciculus (SLF) as the mainly involved fiber tract (for an extension discussion of similar results in different samples see also Fossataro et al., 2018; Pia et al., 2020). In particular, it was found that the lesion disrupts the more ventral component of this fasciculus (i.e., SLF III) connecting temporal areas, including the Extrastriate Body Area (EBA) involved in the visual recognition of the body, and frontal areas, involved in the sensorimotor representation of the body (i.e., the ventral premotor cortex, vPMC) (Errante et al., 2022). We may hypothesize that this fiber tract lesion, together with the selective damage at the middle temporal gyrus (see Figure 17), interrupts the flow of information to and from EBA that are critical for body parts visual processing (Cazzato et al., 2014; Downing & Peelen, 2016; Myers & Sowden, 2008; Urgesi et al., 2004), thus potentially explaining the overall worst performance of E+ patients at the implicit task, as compared to E- patients and Controls. Furthermore, according to different lines of research, employing the RHI in healthy subjects, the normal functioning of a visual-sensorimotor network, mainly involving EBA and vPMC and their functional connectivity, is critical to construct a coherent representation of the bodily self (Gentile et al., 2013; Guterstam et al., 2013; Limanowski & Blankenburg, 2015). Indeed, while we usually distinguish other people's body only by vision, for self-body recognition we might rely on the integration between visual and sensorimotor representations. Coherently, when the connectivity between regions storing visual and sensorimotor representations of the body is disrupted due to a brain damage, as in E+ patients, the ability to visually discriminate between self and others' body parts is lost, as shown by the hyper-attribution effect described in the PE ecological evaluation and mirrored by the present results at the explicit task. Importantly, VLSM performed on the false alarm errors supports this interpretation, showing that lesions involving voxels within SLF are significantly associated with the tendency of committing false alarm errors (Figure 8e).

3.5 References

Bisiach, E., Perani, D., Vallar, G., & Berti, A. (1986). Unilateral neglect: Personal and extra-personal. Neuropsychologia, 24(6), 759–767. https://doi.org/10.1016/0028-3932(86)90075-8

Botvinick, M., & Cohen, J. D. (1998). Rubber hand ‘feels’ what eyes see. Nature, 391(February), 756.

Brugger, P., & Lenggenhager, B. (2014). The bodily self and its disorders: Neurological, psychological and social aspects. Current Opinion in Neurology, 27(6), 644–652. https://doi.org/10.1097/WCO.0000000000000151

Bucchioni, G., Fossataro, C., Cavallo, A., Mouras, H., Neppi-Modona, M., & Garbarini, F. (2016). Empathy or Ownership? Evidence from Corticospinal Excitability during Pain Observation. Journal of Cognitive Neuroscience, 28(11), 1760–1771. https://doi.org/https://doi.org/10.1162/jocn_a_01003

Burin, D., Garbarini, F., Bruno, V., Fossataro, C., Destefanis, C., Berti, A., & Pia, L. (2017). Movements and body ownership: Evidence from the rubber hand illusion after mechanical limb immobilization. Neuropsychologia, 107, 41–47. https://doi.org/10.1016/j.neuropsychologia.2017.11.004

Burin, D., Livelli, A., Garbarini, F., Fossataro, C., Folegatti, A., Gindri, P., & Pia, L. (2015). Are movements necessary for the sense of body ownership? evidence from the rubber hand illusion in pure hemiplegic patients. PLoS ONE, 10(3), 1–12. https://doi.org/10.1371/journal.pone.0117155

Candini, M., Avanzi, S., Cantagallo, A., Zangoli, M. G., Benassi, M., Querzani, P., Lotti, E. M., Iachini, T., & Frassinetti, F. (2018). The lost ability to distinguish between self and other voice following a brain lesion. NeuroImage: Clinical, 18(October 2017), 903–911. https://doi.org/10.1016/j.nicl.2018.03.021

Candini, M., Farinelli, M., Ferri, F., Avanzi, S., Cevolani, D., Gallese, V., Northoff, G., & Frassinetti, F. (2016). Implicit and explicit routes to recognize the own body: Evidence from brain damaged patients. Frontiers in Human Neuroscience, 10(AUG2016). https://doi.org/10.3389/fnhum.2016.00405

Candini, M., Zamagni, E., Nuzzo, A., Ruotolo, F., Iachini, T., & Frassinetti, F. (2014). Who is speaking? Implicit and explicit self and other voice recognition. Brain and Cognition, 92, 112–117. https://doi.org/10.1016/j.bandc.2014.10.001

Cazzato, V., Mian, E., Serino, A., Mele, S., & Urgesi, C. (2014). Distinct contributions of extrastriate body area and temporoparietal junction in perceiving one's own and others' body. Cognitive, Affective and Behavioral Neuroscience, 15(1), 211–228. https://doi.org/10.3758/s13415-014-0312-9

Conson, M., Aromino, A. R., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. Experimental Brain Research, 206(4), 449–453. https://doi.org/10.1007/s00221-010-2418-9

Conson, M., Volpicella, F., De Bellis, F., Orefice, A., & Trojano, L. (2017). "Like the palm of my hands": Motor imagery enhances implicit and explicit visual recognition of one's own hands. Acta Psychologica, 180(September), 98–104. https://doi.org/10.1016/j.actpsy.2017.09.006

Crawford, J. R., & Garthwaite, P. H. (2007). Comparison of a single case to a control or normative sample in neuropsychology: Development of a Bayesian approach. Cognitive Neuropsychology, 24(4), 343–372. https://doi.org/10.1080/02643290701290146

D'Angelo, M., di Pellegrino, G., & Frassinetti, F. (2019). The illusion of having a tall or short body differently modulates interpersonal and peripersonal space. Behavioural Brain Research, 375(June), 112146. https://doi.org/10.1016/j.bbr.2019.112146

D'Angelo, M., Maister, L., Tucciarelli, R., Frassinetti, F., & Longo, M. R. (2020). Embodying an invisible face shrinks the cone of gaze. Journal of Experimental Psychology: General. https://doi.org/10.1037/xge0000953

D'Angelo, M., Pellegrino, G. DI, & Frassinetti, F. (2017). Invisible body illusion modulates interpersonal space. Scientific Reports, 7(1), 1–9. https://doi.org/10.1038/s41598-017-01441-9

De Vignemont, F. (2018). Mind the Body: An Exploration of Bodily Self-Awareness. Oxford University Press, 1–11. https://doi.org/10.1177/0885066610366936

della Gatta, F., Garbarini, F., Puglisi, G., Leonetti, A., Berti, A., & Borroni, P. (2016). Decreased motor cortex excitability mirrors own hand disembodiment during the rubber hand illusion. ELife, 5(OCTOBER2016), 1–14. https://doi.org/10.7554/eLife.14972

Downing, P. E., & Peelen, M. V. (2016). Body selectivity in occipitotemporal cortex: Causal evidence. Neuropsychologia, 83, 138–148. https://doi.org/10.1016/j.neuropsychologia.2015.05.033

Ehrsson, H. H. (2007). The experimental induction of out-of-body experiences. Science, 317(5841), 1048. https://doi.org/10.1126/science.1142175

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., & Garbarini, F. (2022). Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Communications, 4(1), 1–15. https://doi.org/10.1093/braincomms/fcac032

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A sensorimotor network for the bodily self. Journal of Cognitive Neuroscience, 24(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Ferri, F., Frassinetti, F., Costantini, M., & Gallese, V. (2011). Motor simulation and the bodily self. PLoS ONE, 6(3), 1–6. https://doi.org/10.1371/journal.pone.0017927

Folstein, M., Folstein, S., & McHugh, P. (1975). “MINI-MENTAL STATE” A PRACTICAL METHOD FOR GRADING THE COGNITIVE STATE OF PATIENTS FOR THE CLINICIAN. J. Psychiat. Res., 12, 189–198.

Fossataro, C., Bruno, V., Bosso, E., Chiotti, V., Gindri, P., Farnè, A., & Garbarini, F. (2020). The sense of body-ownership gates cross-modal improvement of tactile extinction in brain-damaged patients. Cortex, 127, 94–107. https://doi.org/10.1016/j.cortex.2020.02.004

Fossataro, C., Bruno, V., Gindri, P., Pia, L., Berti, A., & Garbarini, F. (2018). Feeling touch on the own hand restores the capacity to visually discriminate it from someone else’ hand: Pathological embodiment receding in brain-damaged patients. Cortex, 104, 207–219. https://doi.org/10.1016/j.cortex.2017.06.004

Fossataro, C., Gindri, P., Mezzanato, T., Pia, L., & Garbarini, F. (2016). Bodily ownership modulation in defensive responses: Physiological evidence in brain-damaged patients with pathological embodiment of other’s body parts. Scientific Reports, 6(May), 1–11. https://doi.org/10.1038/srep27737

Frassinetti, F., Ferri, F., Maini, M., Benassi, M. G., & Gallese, V. (2011). Bodily self: An implicit knowledge of what is explicitly unknown. Experimental Brain Research, 212(1), 153–160. https://doi.org/10.1007/s00221-011-2708-x

Frassinetti, F., Fiori, S., D'Angelo, V., Magnani, B., Guzzetta, A., Brizzolara, D., & Cioni, G. (2012). Body knowledge in brain-damaged children: A double-dissociation in self and other's body processing. Neuropsychologia, 50(1), 181–188. https://doi.org/10.1016/j.neuropsychologia.2011.11.016

Frassinetti, F., Maini, M., Benassi, M., Avanzi, S., Cantagallo, A., & Farnè, A. (2010). Selective impairment of self body-parts processing in right brain-damaged patients. Cortex, 46(3), 322–328. https://doi.org/10.1016/j.cortex.2009.03.015

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. Journal of Cognitive Neuroscience, 20(8), 1507–1516. https://doi.org/10.1162/jocn.2008.20067

Frassinetti, F., Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., Avanzi, S., & Farnè, A. (2009). Visual processing of moving and static self body-parts. Neuropsychologia, 47(8–9), 1988–1993. https://doi.org/10.1016/j.neuropsychologia.2009.03.012

Galigani, M., Ronga, I., Fossataro, C., Bruno, V., Castellani, N., Sebastiano, A. R., Forster, B., & Garbarini, F. (2021). Like the back of my hand: Visual ERPs reveal a specific change detection mechanism for the bodily self. Cortex, 4. https://doi.org/10.1016/j.cortex.2020.10.014

Gandola, M., Invernizzi, P., Sedda, A., Ferrè, E. R., Sterzi, R., Sberna, M., Paulesu, E., & Bottini, G. (2012). An anatomical account of somatoparaphrenia. Cortex, 48(9), 1165–1178. https://doi.org/10.1016/j.cortex.2011.06.012

Garbarini, F., Fornia, L., Fossataro, C., Pia, L., Gindri, P., & Berti, A. (2014). Embodiment of others' hands elicits arousal responses similar to one's own hands. Current Biology, 24(16), R738–R739. https://doi.org/10.1016/j.cub.2014.07.023

Garbarini, F., Fossataro, C., Berti, A., Gindri, P., Romano, D., Pia, L., della Gatta, F., Maravita, A., & Neppi-Modona, M. (2015). When your arm becomes mine: Pathological embodiment of alien limbs using tools modulates own body representation.

Neuropsychologia, 70, 402–413. https://doi.org/10.1016/j.neuropsychologia.2014.11.008

Garbarini, F., Fossataro, C., Pia, L., & Berti, A. (2020). What pathological embodiment/disembodiment tell us about body representations. Neuropsychologia, 149(October), 107666. https://doi.org/10.1016/j.neuropsychologia.2020.107666

Garbarini, F., & Pia, L. (2013). Bimanual coupling paradigm as an effective tool to investigate productive behaviors in motor and body awareness impairments. Frontiers in Human Neuroscience, 7(NOV), 1–5. https://doi.org/10.3389/fnhum.2013.00737

Garbarini, F., Pia, L., Piedimonte, A., Rabuffetti, M., Gindri, P., & Berti, A. (2013). Embodiment of an alien hand interferes with intact-hand movements. Current Biology, 23(2), R57–R58. https://doi.org/10.1016/j.cub.2012.12.003

Gentile, G., Guterstam, A., Brozzoli, C., & Henrik Ehrsson, H. (2013). Disintegration of multisensory signals from the real hand reduces default limb self-attribution: An fMRI study. Journal of Neuroscience, 33(33), 13350–13366. https://doi.org/10.1523/JNEUROSCI.1363-13.2013

Goble, D. J. (2010). Proprioceptive Acuity Assessment Via Joint Position Matching: From Basic Science to General Practice. Physical Therapy, 90(8), 1176–1184. https://doi.org/10.2522/ptj.20090399

Guterstam, A., Gentile, G., & Ehrsson, H. H. (2013). The Invisible Hand Illusion: Multisensory Integration Leads to the Embodiment of a Discrete Volume of Empty Space. Journal of Cognitive Neuroscience, 25(7), 1078–1099. https://doi.org/10.1162/jocn

Halligan, P. W., Cockburn, J., & WIlson, B. (1991). The behavioural assessment of visual neglect. Neuropsychological Rehabilitation, 1(1), 5–32. https://doi.org/https://doi.org/10.1080/09602019108401377

Hirayama, K., Fukutake, T., & Kawamura, M. (1999). “Thumb localizing test” for detecting a lesion in the posterior column-medial lemniscal system. Journal of the Neurological Sciences, 167(1), 45–49. https://doi.org/10.1016/S0022-510X(99)00136-7

Hua, K., Zhang, J., Wakana, S., Jiang, H., Li, X., Reich, D. S., Calabresi, P. A., Pekar, J. J., van Zijl, P. C. M., & Mori, S. (2008). Tract probability maps in stereotaxic spaces:

Analyses of white matter anatomy and tract-specific quantification. NeuroImage, 39(1), 336–347. https://doi.org/10.1016/j.neuroimage.2007.07.053

Lenggenhager, B., Tadi, T., Metzinger, T., & Blanke, O. (2007). Video Ergo Sum: Manipulating Bodily. Science, 317(August), 1096–1099.

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. Human Brain Mapping, 36(6), 2284–2304. https://doi.org/10.1002/hbm.22770

Longo, M. R., Schüür, F., Kammers, M. P., Tsakiris, M., & Haggard, P. (2009). Self awareness and the body image. Acta psychologica, 132(2), 166-172.

Moro, V., Pernigo, S., Tsakiris, M., Avesani, R., Edelstyn, N. M. J., Jenkinson, P. M., & Fotopoulou, A. (2016). Motor versus body awareness: Voxel-based lesion analysis in anosognosia for hemiplegia and somatoparaphrenia following right hemisphere stroke. Cortex, 83, 62–77. https://doi.org/10.1016/j.cortex.2016.07.001

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. NeuroImage, 42(4), 1669–1677. https://doi.org/10.1016/j.neuroimage.2008.05.045

O’Dowd, A., & Newell, F. N. (2020). The rubber hand illusion is influenced by self-recognition. Neuroscience Letters, 720, 134756.

Petkova, V. I., & Ehrsson, H. H. (2008). If I were you: Perceptual illusion of body swapping. PLoS ONE, 3(12). https://doi.org/10.1371/journal.pone.0003832

Pia, L., Fossataro, C., Burin, D., Bruno, V., Spinazzola, L., Gindri, P., Fotopoulou, K., Berti, A., & Garbarini, F. (2020). The anatomo-clinical picture of the pathological embodiment over someone else’s body part after stroke. Cortex, 130, 203–219. https://doi.org/10.1016/j.cortex.2020.05.002

Pia, L., Garbarini, F., Fossataro, C., Burin, D., & Berti, A. (2016). Sensing the body, representing the body: Evidence from a neurologically based delusion of body ownership. Cognitive Neuropsychology, 33(1–2), 112–119. https://doi.org/10.1080/02643294.2016.1185404

Pia, L., Garbarini, F., Fossataro, C., Fornia, L., & Berti, A. (2013). Pain and body awareness: Evidence from brain-damaged patients with delusional body ownership. Frontiers in Human Neuroscience, 7, 1–9. https://doi.org/10.3389/fnhum.2013.00298

Pia, L., Spinazzola, L., Garbarini, F., Bellan, G., Piedimonte, A., Fossataro, C., Livelli, A., Burin, D., & Berti, A. (2014). Anosognosia for hemianaesthesia: A voxel-based lesion-symptom mapping study. Cortex, 61, 158–166. https://doi.org/10.1016/j.cortex.2014.08.006

Ricci, R., Salatino, A., Garbarini, F., Ronga, I., Genero, R., Berti, A., & Neppi-Mòdona, M. (2016). Effects of attentional and cognitive variables on unilateral spatial neglect. Neuropsychologia, 92, 158–166. https://doi.org/10.1016/j.neuropsychologia.2016.05.004

Romano, D., & Maravita, A. (2019). The dynamic nature of the sense of ownership after brain injury. Clues from asomatognosia and somatoparaphrenia. Neuropsychologia, 132, 107119. https://doi.org/10.1016/j.neuropsychologia.2019.107119

Ronga, I., Garbarini, F., Neppi-Modona, M., Fossataro, C., Pyasik, M., Bruno, V., Sarasso, P., Barra, G., Frigerio, M., Chiotti, V. C., & Pia, L. (2019). “See me, feel me”: Prismatic adaptation of an alien limb ameliorates spatial neglect in a patient affected by pathological embodiment. Frontiers in Psychology, 9(JAN), 1–10. https://doi.org/10.3389/fpsyg.2018.02726

Rorden, C., & Brett, M. (2000). Stereotaxic display of brain lesions. Behavioural Neurology, 12, 191–197. https://doi.org/https://doi.org/10.1155/2000/421719

Rorden, C., Karnath, H. O., & Bonilha, L. (2007). Improving lesion-symptom mapping. Journal of Cognitive Neuroscience, 19(8), 1081–1088. https://doi.org/https://doi.org/10.1162/jocn.2007.19.7.1081

Rossi Sebastiano, A., Poles, K., Miller, L. E., Fossataro, C., Milano, E., Gindri, P., & Garbarini, F. (2022). Reach planning with someone else’s hand. Cortex, 153, 207–219. https://doi.org/10.1016/j.cortex.2022.05.005

Santangelo, G., Siciliano, M., Pedone, R., Vitale, C., Falco, F., Bisogno, R., Siano, P., Barone, P., Grossi, D., Santangelo, F., & Trojano, L. (2015). Normative data for the Montreal Cognitive Assessment in an Italian population sample. Neurological Sciences, 36(4), 585–591. https://doi.org/10.1007/s10072-014-1995-y

Sforza, A., Bufalari, I., Haggard, P., & Aglioti, S. M. (2010). My face in yours: Visuo-tactile facial stimulation influences sense of identity. Social Neuroscience, 5(2), 148–162. https://doi.org/10.1080/17470910903205503

Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. PLoS ONE, 3(12), 2–7. https://doi.org/10.1371/journal.pone.0004040

Tsakiris, M., Hesse, M. D., Boy, C., Haggard, P., & Fink, G. R. (2007). Neural signatures of body ownership: A sensory network for bodily self-consciousness. Cerebral Cortex, 17(10), 2235–2244. https://doi.org/10.1093/cercor/bhl131

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage, 15(1), 273–289. https://doi.org/10.1006/nimg.2001.0978

Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic Stimulation of Extrastriate Body AreaImpairs Visual Processing of Nonfacial Body Parts. Current Biology, 14, 2130–2134. https://doi.org/DOI 10.1016/j.cub.2004.11.031

Vallar, G., & Ronchi, R. (2009). Somatoparaphrenia: A body delusion. A review of the neuropsychological literature. Experimental Brain Research, 192(3), 533–551. https://doi.org/10.1007/s00221-008-1562-y

Zeller, D., Friston, K. J., & Classen, J. (2016). Dynamic causal modeling of touch-evoked potentials in the rubber hand illusion. NeuroImage, 138, 266–273. https://doi.org/10.1016/j.neuroimage.2016.05.065

Zeller, D., Gross, C., Bartsch, A., Johansen-Berg, H., & Classen, J. (2011). Ventral premotor cortex may be required for dynamic changes in the feeling of limb ownership: A lesion study. Journal of Neuroscience, 31(13), 4852–4857. https://doi.org/10.1523/JNEUROSCI.5154-10.2011

Chapter 4. Neural index of self-identity visual recognition: a promising tool for developmental studies

[This research was conducted in collaboration with Dr. Davide Bottari, IMT Lucca. At the time of the writing of the present thesis, these data are unpublished]

4.1 Introduction

In the present Chapter we moved from a developmental level with the aim of developing a protocol in adults to investigate self-hand recognition. Importantly, studying the ability to identify the visual features of the own hand may represent an innovative way to shed light on the neural bases associated to the emergence of bodily-self awareness in infancy. From an ontogenetic point of view, hands might represent the earliest opportunity to distinguish our body from others' bodies, as a result of the uniqueness of sensory sensations that involve our hands. However, so far, the neural mechanisms of bodily-self recognition have been mainly investigated by focusing on the face, due to the prominent role of facial cues in discriminating people identity. Accordingly, numerous studies explored the underpinnings of face identity discrimination and found electrophysiological and neurofunctional signatures of face and self-face recognition both in adults (Jacques & Rossion, 2006; Peelen & Downing, 2007; Sugiura et al., 2015) and in newborns and infants (Buiatti et al., 2019; Farroni et al., 2005; Stapel et al., 2017). In the present study, we focused on self-hand recognition as a neglected yet fundamental line of research for understanding the brain mechanisms subserving bodily-self representation. To characterize the brain dynamics underlying the self-hand recognition, we exploited fast periodic visual stimulation (FPVS). This stimulation protocol takes advantage of the consolidated observation that a visual stimulus presented at a given frequency (e.g., 4Hz) elicits an electrical brain activity precisely at the stimulation rates (i.e., 4Hz), measured with electroencephalography (EEG) (Rossion, 2014). This protocol typically generates high signal-to-noise ratio (SNR) responses, which can be objectively quantified in the frequency-domain, thus providing reliable markers of an automatic visual process, without explicit tasks. In particular, FPVS technique consists in repeating the exact same stimulus (or different stimuli belonging to the same category, e.g. objects) at a rapid frequency rate (base stimuli) and introducing a change of a visual property at a periodic frequency of stimulation (oddball stimulus). The EEG responses elicited at the frequency of the oddball stimulus unambiguously constitutes an index of such change categorization. Indeed, when the brain is able to differentiate base and oddball stimuli, it generates two periodic responses (base and oddball frequency). In contrast, when the change over the dimension of interest is not detected, the brain produces only one periodic response at the base frequency. While FPVS has been traditionally confined to the study of low-level visual processes (for reviews, see Norcia et al., 2015; Rossion et al., 2020), in more recent years it has been extended to assess visual discrimination of more complex images and provided sensitive measures of the processing of body parts, in particular faces (Bottari et al., 2020; Buiatti et al., 2019; de Heering & Rossion, 2015; Dzhelyova et al., 2017; Jacques et al., 2016; Zimmermann et al., 2019).

Here, by combining FPVS with EEG, we presented variable images of others' hands at a 4 Hz stimulation frequency (base stimuli), with images of the self-hand (oddball stimulus) inserted every five images (i.e., 4Hz/5= 0.8 Hz). This main scenario (i.e., *With Self* scenario) is compared with a control scenario (i.e., *Without Self* scenario), in which a constant image of the same other's hand is used as oddball stimulus instead of the self-hand. We expect to identify an implicit marker of self-hand identity recognition, by quantifying greater EEG responses exactly at 0.8 Hz when the oddball stimulus represents the self- than the other-hand. Moreover, since hand identity recognition may be driven by canonical hand orientation (Bucchioni et al., 2016; Conson et al., 2010; Saxe et al., 2006), we also manipulated hand perspective by displaying images of hands in either egocentric perspective (only consistent with looking at one's own body) or allocentric perspective (only consistent with looking at someone else's body). Crucially, we predict that the self-other hand discrimination mechanism is modulated by hand orientation, as possibly revealed by greater discriminative responses to the self-hand when presented in egocentric perspective than allocentric perspective and *viceversa* for the other-hand.

4.2 Materials and Methods

4.2.1 Participants

Eighteen healthy right-handed subjects participated in the study (13 women) aged 20-27 years (mean±SD: 23.83 ±1.79; years of education: 17 ±1.28).

The study was approved by the Ethics Committee of the University of Torino (prot. n°122571) and was conducted in accordance with the seventh revision of the Declaration of Helsinki. Prior to testing, all participants received instructions about the experimental procedure and gave their written informed consent

4.2.2 Stimuli

Visual stimuli consisted of grey-scale pictures (20x20cm) of the dorsum of open right hands belonging either to the participants or to other people (Fig. 18). We took the pictures of hands before the experiment, all in the same room, with controlled illumination conditions and were post-processed. More specifically, we removed the picture background and we replaced it with a black uniform background. Then, we converted original color pictures in grey-scale images with the aim of standardizing different skin colors (for a similar procedure, see e.g. Galigani et al., 2021b; Myers and Sowden, 2008). The resulting visual stimuli were presented at the center of a 24-inches Sony CRT computer screen.

4.2.3 Procedure

Participants sat at a table in a dimly lit room in front of a computer monitor at a viewing distance of 55 cm (screen resolution of 1280 pixels x 1024 pixels at a frame rate of 120 Hz). Stimulus presentation was controlled with Eprime V2.0 software (Psychology Software Tools Inc., Pittsburgh, PA, USA). FPVS was applied, with a squared on-off presentation at the base frequency of 4 Hz and a oddball stimulus was included every five images (0.8 Hz). In two different scenarios, the base stimuli consisted of eight images of different strangers' hands and the oddball stimulus depicted either the self-hand image (i.e., *With Self* scenario) or a constant image of an other-hand (i.e., *Without Self* scenario), which was always different from strangers' hands used as base stimuli (Fig.1). Crucially, we opted to present different images as base stimuli to avoid that eventual oddball responses was merely driven by a low-level perceptual discrimination instead of hand-identity discrimination (for metholodical considerations, see Coll et al., 2019). Visual stimuli were separately presented in egocentric or allocentric perspective, thus yielding four different conditions (Self ego, Self allo, Other ego, Other allo). The order of scenarios was randomized between subjects; moreover, half of the subjects started with the egocentric perspective and the other half with allocentric perspective. Each condition was presented in four consecutive sequences, composed of 300 cycles (75 s per sequence; total of cycles per condition: 1200). Each sequence of stimulation started (fade-in) and ended (fade-out) with a black slide lasting 2 s. These fading periods were intended to avoid abrupt EEG responses at the beginning and end of stimulation (onset and offset visual evoked potentials, surprise reactions from participants or blinks). Participants were instructed to look at the images on the screen and to press the space bar with the right index finger whenever they detected brief (170 ms) changes in the color of the rectangular outline (from purple to red) surrounding the images. These color changes occurred randomly, 21 times per sequence. This task was orthogonal to the manipulation of interest and ensured that participants maintained a constant level of attention throughout the entire experiment (Dzhelyova et al., 2017; Jacques et al., 2016; Zimmermann et al., 2019).

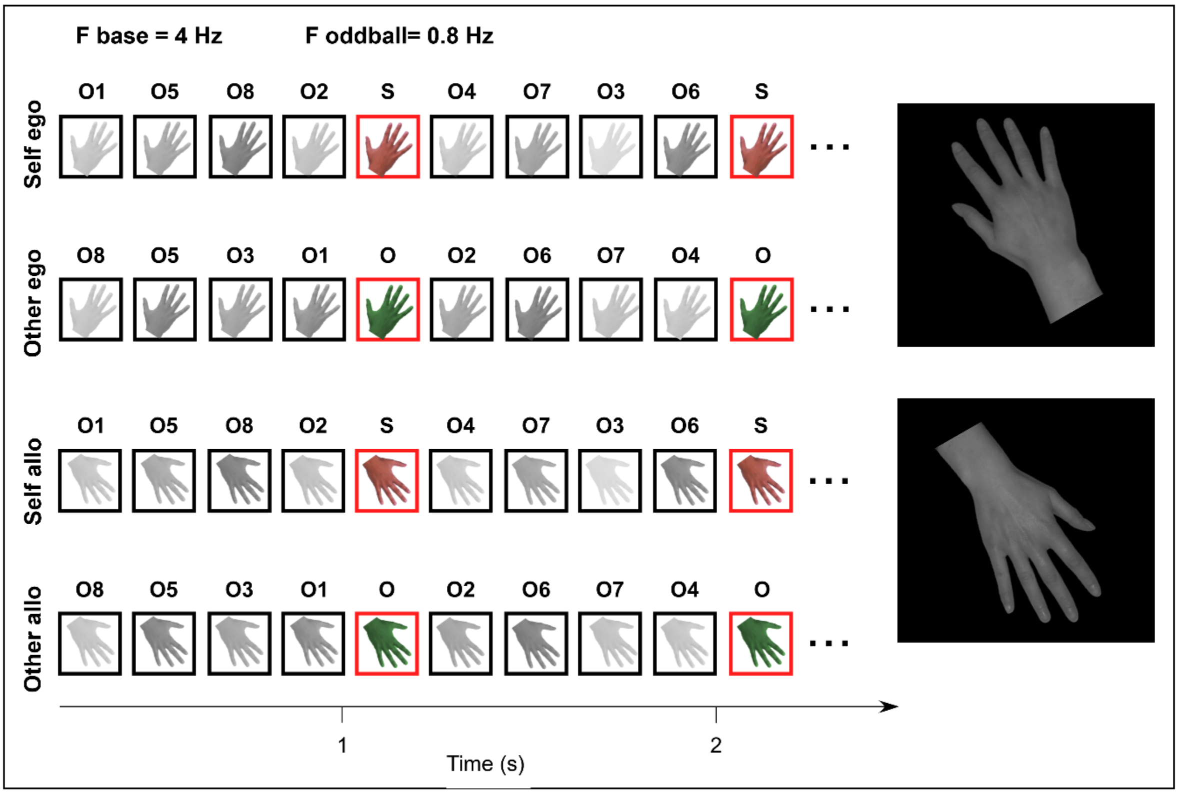


Figure 18. Schematic illustration of the experimental paradigm and the stimuli used in the study. Stimuli were presented at a base frequency of 4 Hz. Oddball stimuli appeared periodically every fifth stimuli, that is, at a rate of 0.8 Hz. Stimuli included grey-colored images of hand, presented in egocentric or allocentric perspective in different blocks. Base stimuli consisted of different strangers’ hands, and the oddball stimuli, according to the experimental block, represented the self-hand or a stranger’s hand (different from those used as base stimuli).

4.2.4 EEG Recording

The electroencephalogram (EEG) was recorded using 32 Ag-AgCl electrodes placed on the scalp according to the International 10-20 system and referenced to the nose.

Electrode impedances were kept below 5 kΩ. To track ocular movements and eye blinks, the electrooculogram was recorded placing two surface electrodes, one placed over the right lower eyelid and the other placed lateral to the outer canthus of the right eye. Continuous EEG was recorded using a *HandyEEG-SystemPLUS Evolution* amplifier (Micromed) and a 1,024 Hz sampling rate. During the experiment, triggers were sent via serial port from the stimulation computer to the EEG recording computer at the beginning and the end of each stimulation sequence. The temporal synchrony between the trigger and the stimulus onset was verified prior to the experiment. Recordings were manually initiated by the experimenter when participants showed artefact-free EEG signals.

4.2.5 Data Analysis

4.2.5.1 Behavioral analysis

For each participant, we calculated the accuracy rate (percentage of correct responses) for the detection of the color change of the rectangular outline in each condition. As control analysis, we run a 2*2 repeated measures ANOVA with Identity (Self and Other), and Perspective (Egocentric and Allocentric) as within subject factors.

4.2.5.2 Frequency domain analysis

All EEG data were analyzed using the free software Letswave 6 (Mouraux & Iannetti, 2008), and MATLAB. Pre-processing procedure was applied in accordance to the most recent studies using FPVS paradigms (Bottari et al., 2020; Retter et al., 2020; Vettori et al., 2020; Zimmermann et al., 2019). Nonetheless, all steps are fully described here.

First, a Butterworth bandpass (fourth-order, 0.1–100 Hz cut-off) and a notch (50 Hz – width=0.5 Hz) filters were applied to EEG raw data, which were down-sampled from 1024 to 512 Hz and segmented from -2 s to 77 s to include 2 s before the first stimulus onset and 2 s after the end of each sequence. EEG recordings were then segmented again from stimulation onset (after 2 s fade-in) until 75 s, corresponding exactly to 300 complete cycles at 4 Hz (76800 bins) to avoid spectral leakage to the neighboring frequencies. Then, the recording sequences of each conditions were concatenated. Biological artifacts due to eye blinks or eye movements were eliminated using a validated method based on an Independent Component Analysis (Jung et al., 2000). Components were extracted and then inspected for their scalp distribution, and distribution across sequences. ICA components indicating one of the artefacts listed above were removed. All channels were finally re-referenced to a common average reference. The concatenates segments were transformed into the frequency domain using a Fast Fourier Transformation (FFT). The FFT transformation yielded a spectrum ranging from 0 to 250 Hz, with a spectral resolution of 1/75=0.013.

To quantify the response of interest, we first identified whether there was a significant response at the frequency of interest (e.g., 0.8 Hz) and its harmonics. To this aim, we computed the FFT grand averaged data across participants and conditions, and then the FFT data was further pooled across all electrodes. z-scores of the frequencies of interest (i.e., 0.8, 1.6, 2.4, etc.) were computed, as in previous studies (e.g., Bottari et al., 2020; Rossion et al., 2015; Verosky et al., 2020; Vettori et al., 2020), using the mean and standard deviation of the 20 surrounding bins (of the frequency of interest). More specifically, z-values were calculated as follows: the amplitude at the frequency of interest *minus* the average of surrounding bins/standard deviation of surrounding bins. We excluded the 2 bins with extreme values and the 2 bins (one on the left and one on the right side) immediately adjacent to the frequency of interest to avoid potential amplitude leakage.

This procedure measures the deviation of the amplitude of the frequency of interest with respect to the mean of the surrounding bins, expressed in terms of standard deviations from this mean. Frequency bins with a z-value larger than 1.64 (corresponding to a one-tailed p-value of $p<0.05$) were considered as deviating significantly from noise. A liberal statistical threshold was used at this stage to select the highest number of harmonics to obtain an accurate quantification of the signal, with a one-tailed testing due to the directionality of the hypothesis. Z-scores were significant (i.e., $z>1.64$) until the eighth harmonic (i.e., until 7.2 Hz - excluding the 4Hz harmonic that was common with the base frequency presentation).

Once significant responses at the frequencies of interest were identified, we returned to the raw single subject data and we computed two measures to describe the response in relation to the noise level: baseline-corrected amplitudes and signal-to-noise ratio (SNR) (Rossion et al., 2020). Only for frequencies which differed from surrounding noise, baseline-corrected amplitudes were calculated by subtracting the value at each frequency bin by the average value of the 20 neighboring frequency bins (10 bins on each side, but excluding the 2 bins directly adjacent and the 2 bins with the most extreme values). Moreover, to better visualize the data SNR was computed in a similar way by dividing the average amplitude of the 20 surrounding bins.

The significant harmonics, identified before with the z-test, were then combined into a summed response at the single participant level. Once the summed oddball response was averaged for each participant, it was used as a dependent measure for further statistical analyses. Since this is the first study with a FPVS approach on self/other hand discrimination, we statistically tested neural discrimination responses at two levels: across the whole scalp (average across all electrodes) and at local regions of interest (ROIs) (see Dzhelyova et al., 2017; Zimmermann et al., 2019 for a similar approach). ROIs were identified using a permutation test on each electrode. In particular, 1000 permutations were run to detect the electrodes wherein the significant effects observed in the whole-scalp analysis survived.

The sum of baseline subtracted amplitudes in each condition was entered in a 2*2 repeated measures ANOVA with Identity (Self and Other), and Orientation (Egocentric and Allocentric) as within subject factors. The ANOVA was run over all electrodes and corrected with a permutation test (n=1000).

As control analyses (see e.g., Bottari et al., 2020), we run a 2*2 repeated measures ANOVA with the response measured at the base frequency (4 Hz and its harmonics, i.e., 8 Hz and 12 Hz) as dependent measure. Statistical analyses were performed using Statistica Software (StatSoft, release 8 RRID:SCR_014213).

4.3 Results

4.3.1 Behavioral results of orthogonal task

The 2*2 ANOVA did not indicate any significant main effect (Identity: $F_{1,17}=0.255$, $p=0.621$; Orientation: $F_{1,17}=1.786$, $p=0.201$) or interaction ($F_{1,17}=0.706$, $p=0.414$), thus showing that accuracy rates for the detection of the color change of the rectangular outline were not different between conditions (mean±SEM: Self ego=96.43±0.68; Self allo=97.69±0.49; Other ego=96.65±0.79; Other allo: 96.94±0.57).

4.3.2 Frequency domain results

The stimulation rate of 0.8 Hz generated a significant ($z>1.64$; $p<0.05$) response at the base frequency at the first eight consecutive harmonics (i.e., 0.8, 1.6, 2.4 and so forth), thus revealing that the hand-identity change have been overall implicitly detected (Fig.19A, 20).

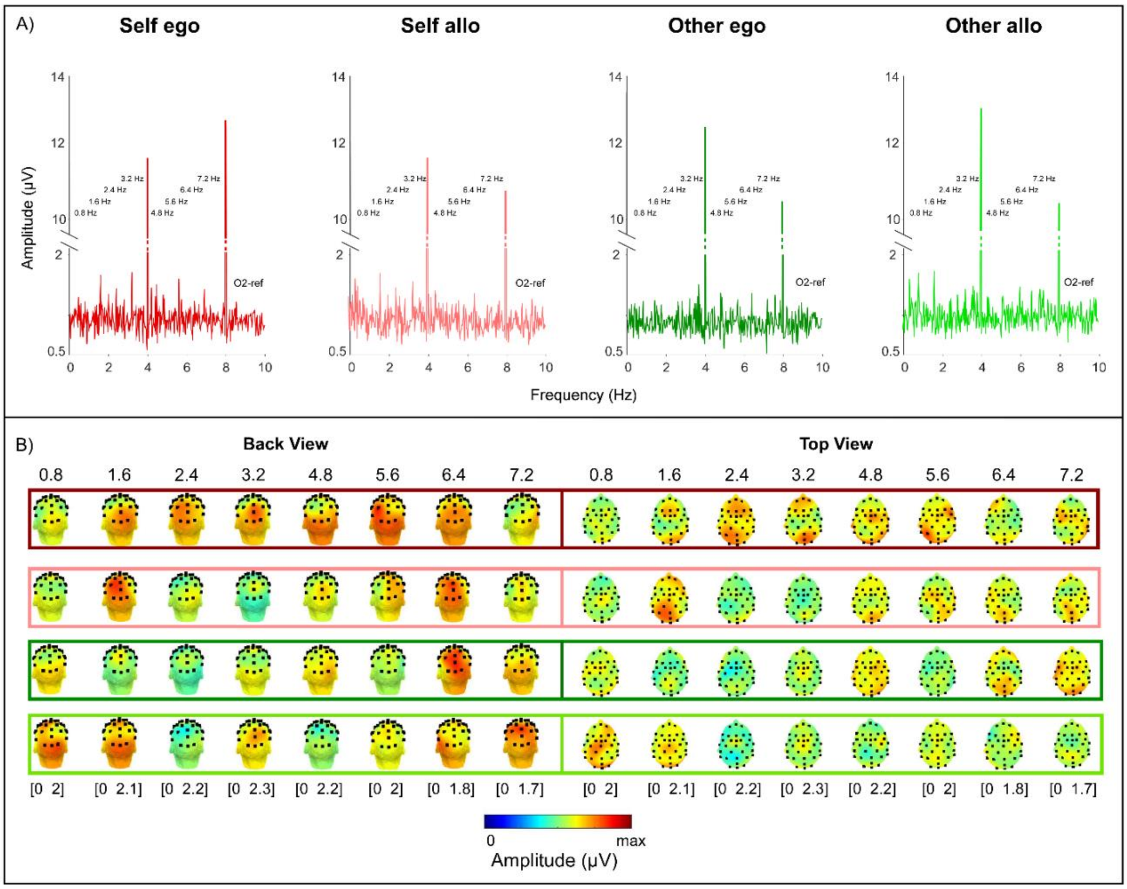


Figure 19. A) Grand-average SNR spectra across posterior-occipital cluster (O1-Oz-O2-P8) in the four different conditions. B) Topographical maps (from back and top views) for each significant harmonics of the oddball frequency. Conditions (identified by the color of the rectangles) are displayed in separate rows and harmonics in separate columns. The common amplitude scale used for each harmonic is reported for each column below the bottom raw of maps.

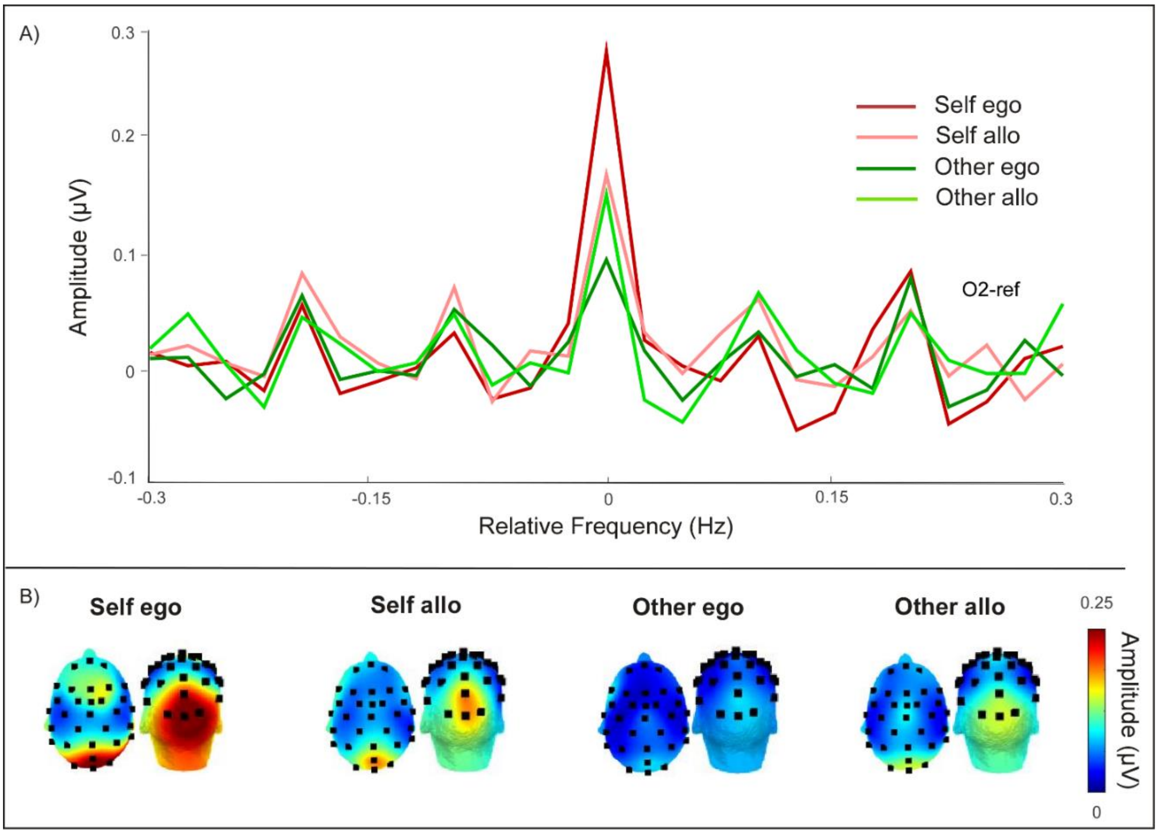


Figure 20. A) The sum of baseline-subtracted chunks depicting the oddball responses at significant harmonics in the four different conditions across posterior-occipital cluster (O1-Oz-O2-P8). B) Topographical maps (from back and top views) of the sum of significant harmonics of the oddball frequency.

Oddball frequency

The ANOVA performed on the responses over all electrodes revealed a significant main effect of Identity on a fronto-central (maximal over Fc2: $F_{1,17}$=6.592, p=0.019) and a posterior-occipital cluster (maximal over O2: $F_{1,17}$=10.387, p=0.005), with enhanced responses to self than other's hand. On the contrary, the main effect of Perspective was not significant over any electrode (p always > 0.125). Crucially, this identity-related visual discrimination is modulated by the canonical perspective of the hand (Identity*Perspective interaction), with the self-hand eliciting greater responses when presented in egocentric (only consistent with looking at one’s own body) than allocentric (only consistent with looking at someone else’s body) perspective and the other-hand showing the opposite pattern. This significant interaction effect was present both over a fronto-central (maximal over F4: $F_{1,17}=6.044$, $p=0.025$) and a posterior-occipital cluster (maximal over O1: $F_{1,17}=5.610$, $p=0.029$). Post-hoc test run on these two clusters showed that the self-hand presented in egocentric perspective as oddball stimulus elicited significative greater responses than all the other conditions (p*s* ranging from 0.002 to 0.030) (Fig. 21).

Base Frequency

As complementary and control analysis, we run two (one per cluster) 2*2 repeated measures ANOVAs on the responses measured at the base frequency with Identity (Self and Other) and Perspective (Egocentric and Allocentric) as within subject factors. The analysis did not reveal neither any significant main effects or interaction (all ps > 0.356).

These results suggest that the brain responses common with all stimuli, which is a mixture of low- and high-level (i.e., shape) visual processes and is projected to the base rate and its harmonics (4 Hz) did not differ between conditions.

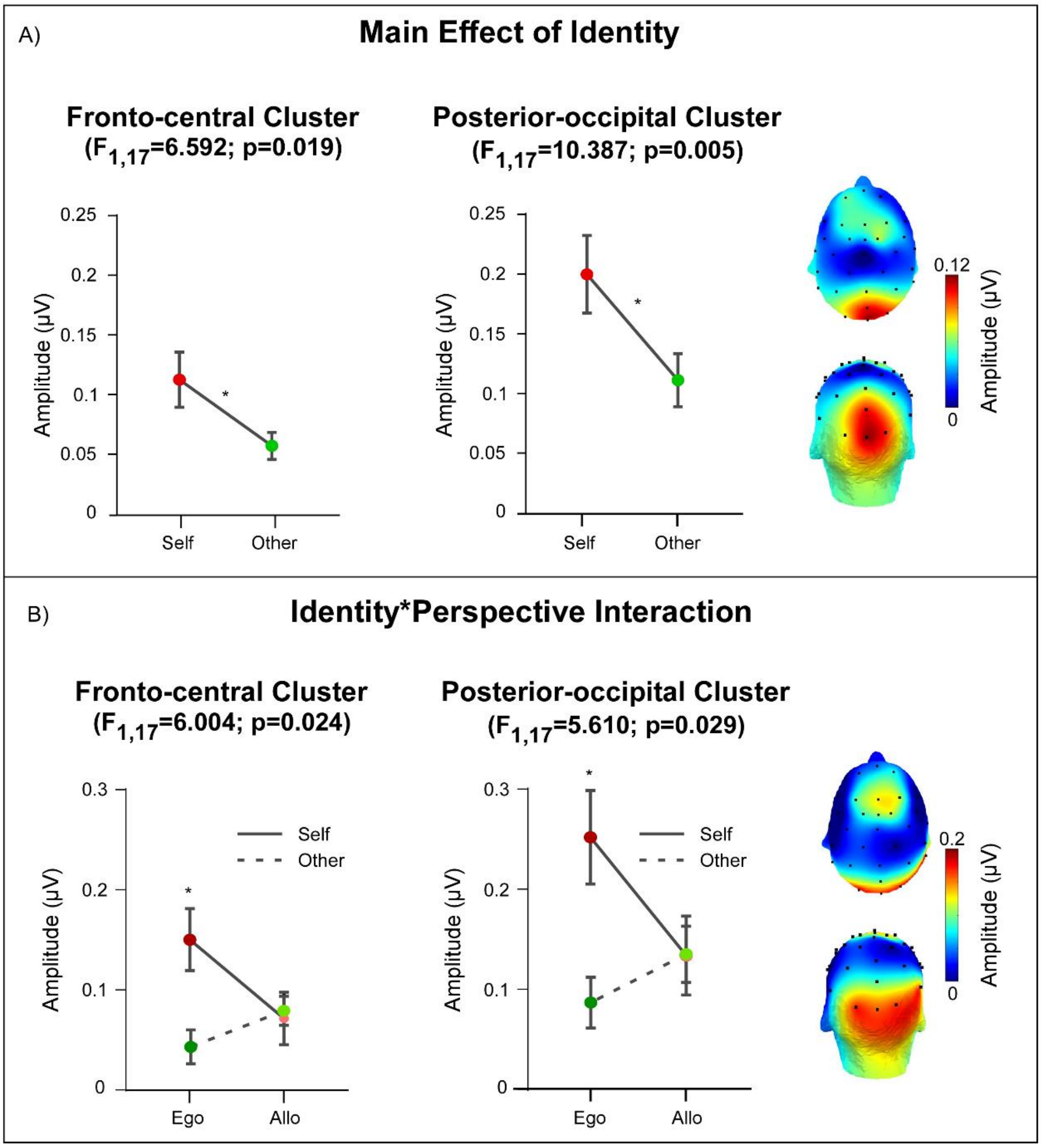


Figure 21. A) Sum of oddball responses across the two clusters of electrodes wherein the Main effect of Identity is significant and the topographical maps of the main effect (top and back views); B) Sum of oddball responses across the two clusters of electrodes wherein the Identity*Perspective interaction is significant and the topographical maps of the interaction effect (top and back views);

4.4 Discussion

Here, we sought to investigate the brain mechanisms sustaining self-hand recognition by employing the fast periodic visual stimulation technique. To this aim, we periodically presented either the participant's hand or a constant hand of a stranger (i.e., oddball stimuli) within a sequence of different strangers' hands images (i.e., base stimuli). This presentation technique splits the neural response evoked by the identity of interest (oddball stimulus: self or other) into a separate response frequency from that of base stimuli. The response that remains observable at the 0.8 Hz identity-specific frequency (i.e., oddball frequency) therefore reflects the isolated response of any population of neurons specifically responsive to the self- or other-hand. Indeed, in this kind of 'oddball-like' paradigm, the common neural response to hands is reflected in the 4 Hz response and its harmonics (8, 12 Hz, etc.), while a 0.8 Hz response emerges only if some neurons specifically coded the periodic change of hand-identity in the stimulation stream (self- or other-hand) (for a similar logic see Rossion et al., 2015 for the categorization between faces and objects; Zimmermann et al., 2019 for the categorization between familiar and unfamiliar faces; Campbell et al., 2020 for the categorization between self and strangers' faces; Lochy et al., 2015 for the categorization between words and pseudowords). Compared to previous EEG studies that have been limited to waveform analysis to indirectly measure processes related to hand recognition (Moreau et al., 2020; Sanabria et al., 2015; Ueda et al., 2022), the FPVS technique allows obtaining direct and robust markers of hand identity-specific processes. Indeed, discriminative responses are objectively observed with a high SNR at the exact frequency predicted by the presentation rate and they are independent from a task, since participants are not instructed to search for any hand identity.

In the present study, the detection of changes in hand-identity was objectively and statistically identified at the specific frequency rate of the identity change (i.e., 0.8 Hz and its harmonics) and this response was distributed over temporo-occipital areas, and over a fronto-central cluster that was mainly associated with responses to the presentation of the self-hand in egocentric perspective (Fig.2-3). In line with a recent study, electrophysiological responses to oddball stimuli depicting hands were smaller than those usually observed when faces are presented (Jacques et al., 2016). Indeed, Jacques and colleagues demonstrated that category-selective responses differed quantitatively between faces and body parts, with a larger (2–4 times) amplitude for faces over the whole scalp.

Our results reveal a fundamental role of hand-identity in driving responses to the oddball stimuli, with significant enhanced responses to the self- than the other-hand (Fig.4). This advantage in processing self than other's body effectors is fully consistent with previous evidence that points out a facilitation in the implicit recognition of the own body, known as *self-advantage* effect (Frassinetti et al., 2008). This effect has been typically described as a behavioral facilitation, with faster reaction times and a greater accuracy in performing implicit tasks that involve self than others' body parts (Candini et al., 2022; Conson et al., 2017; Frassinetti et al., 2009). However, in a recent study we also highlighted an electrophysiological counterpart of the *self-advantage* effect by finding a magnification of electrophysiological mismatch detection responses driven by the implicit self-hand recognition (Galigani et al., 2021).

More critical for the present study, we found that self-hand recognition is modulated by the canonical perspective. In particular, the significant Identity*Perspective interaction compellingly reveals that the perspective of the presented hand affects the identification of the visual features of the hand, with larger responses to the self-hand in egocentric than allocentric perspective and *viceversa* for the other-hand (Fig.4). Despite the higher responses to the self-hand as oddball stimulus may suggest a familiarity bias in our results, this significant modulation of self-hand recognition mechanism driven by perspective excludes this confound. The visual features of the self-hand are undoubtedly more familiar than those of strangers' hands and such familiarity may have contributed to the overall enhanced responses to the own hand regardless of its perspective. Yet, the presence of a discriminative mechanism of self-other hand identity that interacts with perspective cannot be interpreted as a mere familiarity effect. Indeed, we found a facilitation, in terms of boosted responses to the oddball stimuli, that emerges together with the canonical perspective wherein we see such hands in everyday life, with greater neural activity elicited by the self-hand that when presented in egocentric than allocentric perspective and by the other-hand when displayed in allocentric than egocentric perspective. However, in the present study we cannot completely disentangle between an effect driven by self-hand recognition or by a familiarity bias, so in an experiment that we are collecting we are including familiar hands (i.e., partners' hands) as oddball stimuli. We expect to find greater responses to the self-hand than to the familiar hand and we also hypothesize to confirm the recruitment of fronto-central areas only when the self-hand is presented.

Our findings are also consistent with the idea that self-other distinction is strongly grounded in spatial reference frames, since the own body is represented in egocentric coordinates, whereas the other-body in allocentric coordinates (Brady et al., 2011; Pyasik et al., 2022; Tsakiris, 2010). The notion about the role of perspective through which a body-part is observed comes from the broad literature on the embodiment mechanism in healthy subjects and brain-damaged patients. In the rubber hand illusion paradigm, watching a dummy hand being stroked while one's own hidden hand is synchronously stroked can lead to a sense of ownership over the rubber hand (Botvinick & Cohen, 1998;

Ehrsson et al., 2005; Galigani et al., 2022; Limanowski & Blankenburg, 2015; Rossi Sebastiano, Bruno, et al., 2022). Previous studies showed that the dummy hand is not incorporated when it is placed in a third-person perspective, because such position does not match with the postural constraints of the own body (Blanke et al., 2015; Costantini & Haggard, 2007; Petkova et al., 2011; Riemer et al., 2019). Furthermore, it has been recently described in brain-damaged individuals a body ownership delusion, where patients misattribute another's person limb as their own (Errante et al., 2022; Fossataro et al., 2020; Garbarini et al., 2013, 2014; Pia et al., 2020). Interestingly, as for rubber hand illusion, this delusional phenomenon emerges only when the other's hand is perceived in a first-person perspective, thus fitting with the egocentric representation of the own body.

For what concerns spatial localization of our results, we found that the self-other hand discrimination effects were localized over a posterior-occipital and a fronto-central cluster. The posterior distribution is in agreement with the scalp localization of hand-selective responses revealed by electrophysiological (Moreau et al., 2020), neuroimaging (Chan et al., 2004; Myers & Sowden, 2008; Saxe et al., 2006) and brain stimulation studies (De Bellis et al., 2017; Urgesi et al., 2004). This scalp topography may suggest that these responses essentially originate from regions of the visual and extrastriate cortices specifically involved in distinguishing between own and others' hands. Interestingly, the presence of a fronto-central cluster, which was prominent in response to the self-hand (Fig. 3), may indicate the involvement of sensorimotor regions in implicit self-hand recognition. The possible contribution of these areas is compatible with the hypothesis of an integrated, multisensory network devoted to bodily-self recognition (Errante et al., 2022; Ferri et al., 2012a; Limanowski & Blankenburg, 2015). Differently from images depicting others' bodies, which cannot be felt, visual stimuli representing the bodily-self have immediate access also to sensorimotor information. Indeed, from our body we constantly receive motor, somatosensory and proprioceptive afferences in addition to the visual-only information provided by others' bodies. Hence, the present findings may corroborate this view. Indeed we found significant differences also over a fronto-central cluster that may reveal the recruitment of also sensorimotor information in driving self-hand recognition.

To sum up, in the present study, we characterized the dynamics subserving the recognition of the own hand and we demonstrated that i) our brain processes in a privileged way self than other body parts, in line with previous literature (e.g., Frassinetti et al., 2009, 2008; Galigani et al., 2021b); ii) self-hand recognition is modulated by the canonical perspective, thus pointing out the role of perspective in the implicit recognition of the visual features of the hand; iii) the sensorimotor representation of the bodily self might help us to differentiate our own hands from that of others.

Therefore, our results show that FPVS paradigm represents a valid and sensitive tool for measuring in adults high SNR brain responses related to self-other hand discrimination with very short stimulus presentation (around 75 s per condition), thus opening the way to investigate the neural substrates of bodily-self recognition in very special population. In particular, this reliable and sensitive marker can be applied in newborns and infants to shed light on the developmental steps of self-hand recognition.

4.5 References

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. Neuron, 88(1), 145–166. https://doi.org/10.1016/j.neuron.2015.09.029

Bottari, D., Bednaya, E., Dormal, G., Villwock, A., Dzhelyova, M., Grin, K., Pietrini, P., Ricciardi, E., Rossion, B., & Röder, B. (2020). EEG frequency-tagging demonstrates increased left hemispheric involvement and crossmodal plasticity for face processing in congenitally deaf signers. NeuroImage, 223(August). https://doi.org/10.1016/j.neuroimage.2020.117315

Botvinick, M., & Cohen, J. D. (1998). Rubber hand 'feels' what eyes see. Nature, 391(February), 756.

Brady, N., Maguinness, C., & Choisdealbha, Á. N. (2011). My hand or yours? Markedly different sensitivity to egocentric and allocentric views in the hand laterality task. PLoS ONE, 6(8). https://doi.org/10.1371/journal.pone.0023316

Bucchioni, G., Fossataro, C., Cavallo, A., Mouras, H., Neppi-Modona, M., & Garbarini, F. (2016). Empathy or Ownership? Evidence from Corticospinal Excitability during Pain Observation. Journal of Cognitive Neuroscience, 28(11), 1760–1771. https://doi.org/https://doi.org/10.1162/jocn_a_01003

Buiatti, M., Di Giorgio, E., Piazza, M., Polloni, C., Menna, G., Taddei, F., Baldo, E., & Vallortigara, G. (2019). Cortical route for facelike pattern processing in human newborns. Proceedings of the National Academy of Sciences of the United States of America, 116(10), 4625–4630. https://doi.org/10.1073/pnas.1812419116

Campbell, A., Louw, R., Michniak, E., & Tanaka, J. W. (2020). Identity-specific neural responses to three categories of face familiarity (own, friend, stranger) using fast periodic visual stimulation. Neuropsychologia, 141(September 2019), 107415. https://doi.org/10.1016/j.neuropsychologia.2020.107415

Candini, M., Fossataro, C., Pia, L., Vezzadini, G., Gindri, P., Galigani, M., Berti, A., Frassinetti, F., & Garbarini, F. (2022). Bodily self-recognition in patients with pathological embodiment. Journal of Neuroscience Research, 100(11), 1987–2003. https://doi.org/10.1002/jnr.25109

Chan, A. W. Y., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. NeuroReport, 15(15), 2407–2410. https://doi.org/10.1097/00001756-200410250-00021

Coll, M. P., Murphy, J., Catmur, C., Bird, G., & Brewer, R. (2019). The importance of stimulus variability when studying face processing using fast periodic visual stimulation: A novel ‘mixed-emotions’ paradigm. Cortex, 117, 182–195. https://doi.org/10.1016/j.cortex.2019.03.006

Conson, M., Aromino, A. R., & Trojano, L. (2010). Whose hand is this? Handedness and visual perspective modulate self/other discrimination. Experimental Brain Research, 206(4), 449–453. https://doi.org/10.1007/s00221-010-2418-9

Conson, M., Volpicella, F., De Bellis, F., Orefice, A., & Trojano, L. (2017). “Like the palm of my hands”: Motor imagery enhances implicit and explicit visual recognition of one’s own hands. Acta Psychologica, 180(September), 98–104. https://doi.org/10.1016/j.actpsy.2017.09.006

Costantini, M., & Haggard, P. (2007). The rubber hand illusion: Sensitivity and reference frame for body ownership. Consciousness and Cognition, 16(2), 229–240. https://doi.org/10.1016/j.concog.2007.01.001

De Bellis, F., Trojano, L., Errico, D., Grossi, D., & Conson, M. (2017). Whose hand is this? Differential responses of right and left extrastriate body areas to visual images of self and others’ hands. Cognitive, Affective and Behavioral Neuroscience, 17(4), 826–837. https://doi.org/10.3758/s13415-017-0514-z

de Heering, A., & Rossion, B. (2015). Rapid categorization of natural face images in the infant right hemisphere. ELife, 4(JUNE), 1–14. https://doi.org/10.7554/eLife.06564

Dzhelyova, M., Jacques, C., & Rossion, B. (2017). At a single glance: Fast periodic visual stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in the human brain. Cerebral Cortex, 27(8), 4106–4123. https://doi.org/10.1093/cercor/bhw223

Ehrsson, H. H., Holmes, N. P., & Passingham, R. E. (2005). Touching a rubber hand: Feeling of body ownership is associated with activity in multisensory brain areas. Journal of Neuroscience, 25(45), 10564–10573. https://doi.org/10.1523/JNEUROSCI.0800-05.2005

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., & Garbarini, F. (2022). Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Communications, 4(1), 1–15. https://doi.org/10.1093/braincomms/fcac032

Farroni, T., Johnson, M. H., Menon, E., Zulian, L., Faraguna, D., & Csibra, G. (2005). Newborns’ preference for face-relevant stimuli: Effects of contrast polarity. Proceedings of the National Academy of Sciences of the United States of America, 102(47), 17245–17250. https://doi.org/10.1073/pnas.0502205102

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012). A sensorimotor network for the bodily self. Journal of Cognitive Neuroscience, 24(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Fossataro, C., Bruno, V., Bosso, E., Chiotti, V., Gindri, P., Farnè, A., & Garbarini, F. (2020). The sense of body-ownership gates cross-modal improvement of tactile extinction in brain-damaged patients. Cortex, 127, 94–107. https://doi.org/10.1016/j.cortex.2020.02.004

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. Journal of Cognitive Neuroscience, 20(8), 1507–1516. https://doi.org/10.1162/jocn.2008.20067

Frassinetti, F., Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., Avanzi, S., & Farnè, A. (2009). Visual processing of moving and static self body-parts. Neuropsychologia, 47(8–9), 1988–1993. https://doi.org/10.1016/j.neuropsychologia.2009.03.012

Galigani, M., Fossataro, C., Gindri, P., Conson, M., & Garbarini, F. (2022). Monochannel Preference in Autism Spectrum Conditions Revealed by a Non-Visual Variant of Rubber Hand Illusion. Journal of Autism and Developmental Disorders, 52(10), 4252–4260. https://doi.org/10.1007/s10803-021-05299-9

Galigani, M., Ronga, I., Fossataro, C., Bruno, V., Castellani, N., Sebastiano, A. R., Forster, B., & Garbarini, F. (2021). Like the back of my hand: Visual ERPs reveal a specific change detection mechanism for the bodily self. Cortex, 4. https://doi.org/10.1016/j.cortex.2020.10.014

Garbarini, F., Fornia, L., Fossataro, C., Pia, L., Gindri, P., & Berti, A. (2014). Embodiment of others' hands elicits arousal responses similar to one's own hands. Current Biology, 24(16), R738–R739. https://doi.org/10.1016/j.cub.2014.07.023

Garbarini, F., Pia, L., Piedimonte, A., Rabuffetti, M., Gindri, P., & Berti, A. (2013). Embodiment of an alien hand interferes with intact-hand movements. Current Biology, 23(2), R57–R58. https://doi.org/10.1016/j.cub.2012.12.003

Jacques, C., Retter, T. L., & Rossion, B. (2016). A single glance at natural face images generate larger and qualitatively different category-selective spatio-temporal signatures than other ecologically-relevant categories in the human brain. NeuroImage, 137, 21–33. https://doi.org/10.1016/j.neuroimage.2016.04.045

Jacques, C., & Rossion, B. (2006). The speed of individual face categorization. Psychological Science, 17(6), 485–492. https://doi.org/10.1111/j.1467-9280.2006.01733.x

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. Human Brain Mapping, 36(6), 2284–2304. https://doi.org/10.1002/hbm.22770

Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. Neuropsychologia, 66, 18–31. https://doi.org/10.1016/j.neuropsychologia.2014.11.007

Moreau, Q., Parrotta, E., Era, V., Martelli, M. L., & Candidi, M. (2020). Role of the occipito-temporal theta rhythm in hand visual identification. Journal of Neurophysiology, 123(1), 167–177. https://doi.org/10.1152/jn.00267.2019

Mouraux, A., & Iannetti, G. D. (2008). Across-trial averaging of event-related EEG responses and beyond. Magnetic Resonance Imaging, 26(7), 1041–1054. https://doi.org/10.1016/j.mri.2008.01.011

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. NeuroImage, 42(4), 1669–1677. https://doi.org/10.1016/j.neuroimage.2008.05.045

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady state VEP in research. Journal of Vision, 15(6), 1–46. https://doi.org/10.1167/15.6.4.doi

Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. Nature Reviews Neuroscience, 8(8), 636–648. https://doi.org/10.1038/nrn2195

Petkova, V. I., Khoshnevis, M., & Ehrsson, H. H. (2011). The perspective matters! Multisensory integration in egocentric reference frames determines full-body ownership. Frontiers in Psychology, 2(MAR), 1–7. https://doi.org/10.3389/fpsyg.2011.00035

Pia, L., Fossataro, C., Burin, D., Bruno, V., Spinazzola, L., Gindri, P., Fotopoulou, K., Berti, A., & Garbarini, F. (2020). The anatomo-clinical picture of the pathological embodiment over someone else’s body part after stroke. Cortex, 130, 203–219. https://doi.org/10.1016/j.cortex.2020.05.002

Pyasik, M., Fortunato, E., Dal Monte, O., Schintu, S., Garbarini, F., Ciorli, T., & Pia, L. (2022). Self-other distinction modulates the social softness illusion. Psychological Research, 86(4), 1165–1173. https://doi.org/10.1007/s00426-021-01549-8

Retter, T. L., Jiang, F., Webster, M. A., & Rossion, B. (2020). All-or-none face categorization in the human brain. NeuroImage, 213(February), 116685. https://doi.org/10.1016/j.neuroimage.2020.116685

Riemer, M., Trojan, J., Beauchamp, M., & Fuchs, X. (2019). The rubber hand universe: On the impact of methodological differences in the rubber hand illusion. Neuroscience and

Biobehavioral Reviews, 104(January), 268–280. https://doi.org/10.1016/j.neubiorev.2019.07.008

Rossi Sebastiano, A., Bruno, V., Ronga, I., Fossataro, C., Galigani, M., Neppi-Modona, M., & Garbarini, F. (2022). Diametrical modulation of tactile and visual perceptual thresholds during the rubber hand illusion: a predictive coding account. Psychological Research, 86(6), 1830–1846. https://doi.org/10.1007/s00426-021-01608-0

Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. Experimental Brain Research, 232(6), 1599–1621. https://doi.org/10.1007/s00221-014-3934-9

Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. European Journal of Neuroscience, 52(10), 4283–4344. https://doi.org/10.1111/ejn.14865

Rossion, B., Torfs, K., Jacques, C., & Liu-Shuang, J. (2015). Fast periodic presentation of natural images reveals a robust face-selective electrophysiological response in the human brain. Journal of Vision, 15(1), 1–18. https://doi.org/10.1167/15.1.18

Sanabria, D., Madrid, E., Aranda, C., & Ruz, M. (2015). Attentional orienting to own and others' hands. Experimental Brain Research, 233(8), 2347–2355. https://doi.org/10.1007/s00221-015-4303-z

Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. Cerebral Cortex, 16(2), 178–182. https://doi.org/10.1093/cercor/bhi095

Stapel, J. C., van Wijk, I., Bekkering, H., & Hunnius, S. (2017). Eighteen-month-old infants show distinct electrophysiological responses to their own faces. Developmental Science, 20(5). https://doi.org/10.1111/desc.12437

Sugiura, M., Miyauchi, C. M., Kotozaki, Y., Akimoto, Y., Nozawa, T., Yomogida, Y., Hanawa, S., Yamamoto, Y., Sakuma, A., Nakagawa, S., & Kawashima, R. (2015). Neural mechanism for mirrored self-face recognition. Cerebral Cortex, 25(9), 2806–2814. https://doi.org/10.1093/cercor/bhu077

Tsakiris, M. (2010). My body in the brain: A neurocognitive model of body-ownership. Neuropsychologia, 48(3), 703–712. https://doi.org/10.1016/j.neuropsychologia.2009.09.034

Ueda, M., Ueno, K., Inamoto, T., Shiroma, C., Hata, M., Ishii, R., & Naito, Y. (2022). Parietal Gamma Band Oscillation Induced by Self-Hand Recognition. Brain Sciences, 12(2). https://doi.org/10.3390/brainsci12020272

Urgesi, C., Berlucchi, G., & Aglioti, S. M. (2004). Magnetic Stimulation of Extrastriate Body AreaImpairs Visual Processing of Nonfacial Body Parts. Current Biology, 14, 2130–2134. https://doi.org/DOI 10.1016/j.cub.2004.11.031

Verosky, S. C., Zoner, K. A., Marble, C. W., Sammon, M. M., & Babarinsa, C. O. (2020). Familiarization increases face individuation measured with fast periodic visual stimulation. Biological Psychology, 153(March), 107883. https://doi.org/10.1016/j.biopsycho.2020.107883

Vettori, S., Dzhelyova, M., Van der Donck, S., Jacques, C., Van Wesemael, T., Steyaert, J., Rossion, B., & Boets, B. (2020). Combined frequency-tagging EEG and eye tracking reveal reduced social bias in boys with autism spectrum disorder. Cortex, 125, 135–148. https://doi.org/10.1016/j.cortex.2019.12.013

Zimmermann, F. G. S., Yan, X., & Rossion, B. (2019). An objective, sensitive and ecologically valid neural measure of rapid human individual face recognition. Royal Society Open Science, 6(6). https://doi.org/10.1098/rsos.181904

Everywhere in the world,
self starts with body.
Roy Baumeister

General conclusions

The present thesis aimed to investigate the brain dynamics subserving bodily-self recognition, by exploiting electrophysiological and behavioral measures both in the health and pathological brain.

In the last decades self-recognition has been mainly studied shedding light on the neural underpinnings of face-recognition. Indeed, the face constitutes the preferential body-part that conveys crucial information about a person's identity. Coherently, in literature there is a huge amount of evidence that clarified the neural mechanisms involved in the discrimination between the self-face and others' faces (e.g., Kaplan et al., 2008; Keyes et al., 2010; Rubianes et al., 2021; Sugiura et al., 2008, 2015; Tsakiris, 2008). However, in the present work, we adopted a different approach by focusing on the hand. The hand represents a crucial body-parts that also allows to distinguish our body from others' bodies. Indeed, our hands constantly receive unique multisensory whose association and integration may play a crucial role in developing a sense of bodily-self (Blanke et al., 2015; De Klerk et al., 2021; Ferri et al., 2012b).

The works presented in this thesis lay the foundations on the pioneering studies of Frassinetti and collaborators. The authors described for the first-time the so-called self-advantage effect, which consists of a more efficient behavioral performance when doing a task involving self than others' hands (Ferri et al., 2012b; Frassinetti et al., 2008, 2009). They also explored the presence of this effect in brain-damaged patients, demonstrating that distinct hemispheric lesions affect differently the ability to recognize the own body

(Frassinetti et al., 2010). Overall, these results suggest that the dynamics involved in self than other hand recognition are different and that the visual identification of the own hand recruit specific and dedicated brain networks. But, *which are the brain mechanisms subserving self-hand recognition*? This thesis aimed at answering to this question, by also exploring whether the this unique multisensory representation of the hand plays a crucial role in bodily-self recognition.

In Chapter 1, we identified a marker of self/other hand discrimination that constitutes an electrophysiological marker of the self-advantage effect (Frassinetti et al., 2008, 2009), by taking advantage of the mismatch detection phenomenon that is revealed by a greater amplitude when a change is detected within the stimulation stream (Ronga et al., 2013; Torta et al., 2012; Tugin et al., 2016; Zhang et al., 2013). We presented images pairs of different of identical stimuli including the self and others' hands to verify whether implicit bodily-self recognition is able to modulate change detection responses. Crucially, we found significantly different ERP amplitude modulation between repeated and non-repeated conditions only when the self-hand was presented, thus revealing the relevance of bodily-self recognition in boosting the mismatch detection phenomenon. Our results confirm the salience of the self-hand, as demonstrated by its ability to revert repetition suppression effectively. Interestingly, such salience of self-recognition turns up even when entailing the implicit identification of body effectors, selectively through their visual appearances. Apparently, recognizing our own body seems to represent an aprioristic relevant matter for the individual, independently from specific task instructions. The specificity observed for self-hand recognition in our data suggests that the self has a systematic processing advantage, likely related to its inherent multimodal dimension.

Then, based on the results of the experiment of Chapter 1, we employed a twofold approach (Chapter 2: healthy subjects; Chapter 3: brain-damaged patients) to explore whether bodily-self recognition relies on an integrated and multisensory network.

In Chapter 2, we investigated the involvement of the primary somatosensory cortex in the implicit recognition of the self-hand. In this study we presented the very same visual stimuli of Chapter 1, but we included half of the trials where we administered also concomitant tactile stimulation to both hands. In this way, we exploited a recent protocol that entails the subtraction of visual activity from visual-tactile activity (i.e., Vep-free Seps) to examine visually-driven processing of information in cortices other than visual areas (Arslanova et al., 2019; Galvez-Pol et al., 2018, 2020; Sel et al., 2014). With this electrophysiological approach we were able to test the hypothesis of an involvement of tactile information in bodily-self identification. Our results confirm this hypothesis, since we found that the visual presentation of the self-hand significantly magnified somatosensory activity as compared to the other-hand. Despite the tactile stimuli were the very same (for what concerns location, intensity and duration) across conditions, somatosensory evoked potential were greater when tactile stimuli were coupled with the image of the own hand than the image of an other’s hand. Interestingly, our data indicates that the bodily self has a systematic influence on the somatosensory system. Differently from images depicting others' bodies, which cannot be felt, visual stimuli representing the bodily-self may have a preferential access to somatosensory information and it is in line with this view that the nervous system relies on the integration between visual features and sensory information to recognize the bodily self (Ferri et al., 2012a; Limanowski & Blankenburg, 2015).

In Chapter 3, we further test the hypothesis of the role of a multimodal network in subserving bodily-self recognition by capitalizing on brain-damaged patients. In particular, we test patients affected by pathological embodiment (also called E+

patients); these patients, during the ecological evaluation, misattribute another person's limb as their own, thus revealing a possible impaired visual self-other discrimination. In behavioral tasks, E+, E- (patients without pathological embodiment) and controls had to implicitly and explicitly recognize the own hand. We found a worst ability of E+ patients in recognizing self body effectors than E- and controls. Crucially, this behavioral performance was associated with the lesions involving the superior longitudinal fasciculus connecting temporal areas, including the Extrastriate Body Area (EBA) involved in the visual recognition of the body, and frontal areas, involved in the sensorimotor representation of the body (i.e., the ventral premotor cortex, vPMC) (Errante et al., 2022; Pia et al., 2020).

In Chapter 4, we aimed to develop a sensitive protocol in adults to identify an implicit marker of self-hand recognition suitable to be applied to newborns and infants. To this aim we exploited FPVS (Bottari et al., 2020; Dzhelyova et al., 2017; Norcia et al., 2015; Rossion et al., 2020; Zimmermann et al., 2019), that allows to obtain sensitive and reliable measures in few minutes only, thus complying, for future studies, with the short visual attentions of newborns and infants. With this study, we demonstrated that our FPVS paradigm represents a valid and sensitive tool for measuring in adults reliable brain responses related to self-other hand discrimination, Indeed, we found that periodic oddball responses are greater in response to the self-hand than to others' hands and that the perspective of the presented hand affects the identification of the visual features of the hand.

Taken together, all the results described in the present project demonstrate that self-hand recognition recruit different strategies and different brain mechanisms than other-hand recognition. In particular, our results seem to be in line with the tenet that visual information is not enough *per se* to drive implicit body-self recognition. Multiple sensory cues play a role the recognition of the own hand because it is the matching of visual, tactile, motor and proprioceptive information originating from the same body part that contributes to an intermodal sensory image of the body (Jeannerod, 2003). Relevant literature stressed a prevalent role of vision over other senses in self-recognition. For instance, the studies on RHI reveal that we feel our hand where we see it, not the opposite (Botvinick & Cohen, 1998). By contrast, when the participants attribute the dummy and to themselves, the functional connectivity between visual areas (e.g. lateral occipitotemporal cortex and extrastriate body area; EBA) and ventral premotor cortex is specifically reinforced (Limanowski & Blankenburg, 2015; Zeller et al., 2016), thus revealing that the interplay between visual and sensorimotor areas is critical in body ownership. Furthermore, it has been proposed that EBA is selectively involved in self/other distinction, but the results are very controversial. Myers and Sowden (2008) found a greater adaptation in blocks only comprising views of other hands, as compared to blocks comprising views of both self and other hands, thus suggesting that EBA holds populations of neurons that differently respond to self and other hand images. Yet, other results seem to confirm the view of Downing and Peeling (2011) who advocated that EBA is not involved in any high-level function, but only encode fine details about visually perceived bodies. According to this hypothesis, several studies reported no differences when contrasting, in fMRI studies, self and other images (hand or body) (Devue et al., 2007; Hodzic et al., 2009; Saxe et al., 2006; Vocks et al., 2010). Moreover, another approach to test whether EBA primarily encodes the self or the other is to test the effect of viewpoint: if EBA would preferentially respond to one’s own body parts, it should expect a stronger response to body parts presented in a first person perspective, while stronger responses to third person perspective would be expected if this region is primarily involved in the encoding of others’ bodies. The two studies that have manipulated viewpoint both found slightly stronger responses in right EBA to bodies presented in third person view (Chan et al., 2004; Saxe et al., 2006), inconsistent with the preference for one's own body reported by some of the studies discussed above. Also TMS studies provide incongruent evidence, so that different stimulation protocols and different tasks led to different results that do not allow to confirm that EBA is directly involved in self/other hand-body distinction (De Bellis et al., 2017; Pann et al., 2021). The results proposed in the present thesis are more in line with the idea that visual areas responsive to bodily stimuli provide specialized information about the form and configuration of bodies to other regions that extract and make explicit the meaningful signals of the body, making possible the identity discrimination. In this framework, visual areas create a perceptual representation of the shape of body-parts that are used by other brain regions to represent self-identity (Downing & Peelen, 2011; Ferri et al., 2012; Frassinetti et al., 2011). Thus, EBA, for instance, participates in the early phase of the visual processing of the presented body-part but ownership distinction is likely processed upstream, in other cortical areas associated with self/other distinction. Accordingly, self-face recognition has not been linked only to visual regions, but to a broad network encompassing fronto-parietal areas (Kaplan et al., 2008; Minnebusch & Daum, 2009; Morita et al., 2017; Platek et al., 2008; Sugiura et al., 2015; Uddin et al., 2005). So, we also believe that the recognition of the own hand involves sensory and motor cortices. Specifically, the involved sensory cortices are related to the sensory modalities relevant to the stimulus or representation: vision, but also somatic sensation and motor information (Ferri et al., 2012a; Sugiura, 2015). Indeed, we do not have a merely visual representation of our hands, since from them we constantly receive also motor, tactile and proprioceptive efferences. So, we hypothesize that the enhanced somatosensory activity elicited by implicit self-hand recognition (Chapter 2) and the presence of a fronto-central cluster when discriminating between self and other hand (Chapter 4) reflects the fact that the image of the hand contains also sensorimotor information. In this way, we propose that when we are presented with images of our hand, visual and extrastriate areas extrapolate body-related information and project to sensorimotor cortices that allows to recognize the own body. Also our findings in Chapter 3 support the idea that the flow of information between visual and sensorimotor areas is crucial in bodily-self recognition. Indeed, only patients with lesion of fiber tracts connecting posterior and anterior regions exhibit an impairment in identifying self body-parts. In line with this, Beck and colleagues demonstrated that interfering with the communication between EBA and S1, by disrupting the activity of hVIP, attenuated personal visual enhancement of touch (i.e., the increase of tactile acuity when simultaneously seeing the own hand) but did not affect interpersonal VET (i.e., the increase of tactile acuity when simultaneously seeing the own hand) (Beck et al., 2015). Also, in a recent study on monkeys it has been provided neural evidence of mirror self-recognition in the primate SII, supporting the involvement of somatosensory areas in the establishment of bodily self-consciousness and in distinguishing self and non-self (Bretas et al., 2021).

To sum up, our findings may contribute to clarify that the multisensory representation of the hand constitutes is directly responsible for its implicit recognition. Indeed, from our hands we constantly receive several multisensory efferences, including tactile, visual, motor and proprioceptive information that are continuously associated in our brain. This association between somatosensory and visual information may be the mechanism through which a sense of self is developed, because only the hand on which multisensory signals converge is “mine”. This evidence opens the way to investigate the emergence of body representation in infants by focusing on the ability of visually recognizing the self hand. Indeed, during the ontogenetic development hands represent an important medium through which we come in contact with others and the external world, as well as feet that are likewise recognized exploiting visuo-motor associations (self-produced movements and associated auditory stimuli) within the four month of life (Rochat & Morgan, 1998).

Consequently, the hand may represent one of the earliest opportunity to distinguish our from others' body and to develop a primitive sense of bodily-self. This line of research would be innovative within the developmental domain, since, so far, a large number of studies investigated the development of face visual recognition (e.g., Bahrick et al., 1996; Rochat and Striano, 2000; Stapel et al., 2017 - see Rochat & Morgan, 1998 for leg recognition). These studies provided evidence that the ability to visually identify one's own facial features as being part of the self develops at around 18-24 months of age, but we strongly believe that the visual recognition of the own hand may emerge earlier in life. Indeed, babies start staring at the own hand as a functional step to develop visually-guided actions and interact with objects and people. In the first 6 months, since infants frequently engage in "pre-reaching" movements (Rochat, 1989; Von Hofsten & Lindhagen, 1979), they intensively gaze at their hands, thus associating the sensorimotor feedback with the hands' visual features. In this way, only the visual details that are simultaneously associated with sensorimotor representations (i.e., originating from movement perception, position sense, and tactile sensation) can be gradually recognized as belonging to the self-hand and discriminated from the others' hands (i.e., belonging to adults and peers). Therefore, we think that establishing such sensorimotor contingencies in the motor context may allow self-hand recognition to develop by the first year of life, thereby earlier than the emergence of self-face identification that cannot prescind from a persisted looking in a mirror.

References

Arslanova, I., Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2019). Searching for bodies: ERP evidence for independent somatosensory processing during visual search for body-related information. NeuroImage, 195(March), 140–149. https://doi.org/10.1016/j.neuroimage.2019.03.037

Bahrick, L., Moss, L., & Fadil, C. (1996). Development of visual self-recognition in infancy. Ecological Phychology, 8(3), 189–208. https://doi.org/https://doi.org/10.1207/s15326969eco0803_1

Beck, B., Bertini, C., Haggard, P., & Làdavas, E. (2015). Dissociable routes for personal and interpersonal visual enhancement of touch. Cortex, 73, 289–297. https://doi.org/10.1016/j.cortex.2015.09.008

Blanke, O., Slater, M., & Serino, A. (2015). Behavioral, Neural, and Computational Principles of Bodily Self-Consciousness. Neuron, 88(1), 145–166. https://doi.org/10.1016/j.neuron.2015.09.029

Bottari, D., Bednaya, E., Dormal, G., Villwock, A., Dzhelyova, M., Grin, K., Pietrini, P., Ricciardi, E., Rossion, B., & Röder, B. (2020). EEG frequency-tagging demonstrates increased left hemispheric involvement and crossmodal plasticity for face processing in congenitally deaf signers. NeuroImage, 223(August). https://doi.org/10.1016/j.neuroimage.2020.117315

Botvinick, M., & Cohen, J. D. (1998). Rubber hand ‘feels’ what eyes see. Nature, 391(February), 756.

Bretas, R., Taoka, M., Hihara, S., Cleeremans, A., & Iriki, A. (2021). Neural evidence of mirror self-recognition in the secondary somatosensory cortex of macaque: Observations from a single-cell recording experiment and implications for consciousness. Brain Sciences, 11(2), 1–12. https://doi.org/10.3390/brainsci11020157

Chan, A. W. Y., Peelen, M. V., & Downing, P. E. (2004). The effect of viewpoint on body representation in the extrastriate body area. NeuroReport, 15(15), 2407–2410. https://doi.org/10.1097/00001756-200410250-00021

De Bellis, F., Trojano, L., Errico, D., Grossi, D., & Conson, M. (2017). Whose hand is this? Differential responses of right and left extrastriate body areas to visual images of self and others’ hands. Cognitive, Affective and Behavioral Neuroscience, 17(4), 826–837. https://doi.org/10.3758/s13415-017-0514-z

De Klerk, C. C. J. M., Filippetti, M. L., & Rigato, S. (2021). The development of body representations: An associative learning account. Proceedings of the Royal Society B: Biological Sciences, 288(1949). https://doi.org/10.1098/rspb.2021.0070

Devue, C., Collette, F., Balteau, E., Degueldre, C., Luxen, A., Maquet, P., & Brédart, S. (2007). Here I am: The cortical correlates of visual self-recognition. Brain Research, 1143(1), 169–182. https://doi.org/10.1016/j.brainres.2007.01.055

Downing, P. E., & Peelen, M. V. (2011). The role of occipitotemporal body-selective regions in person perception. Cognitive Neuroscience, 2(3–4), 186–203. https://doi.org/10.1080/17588928.2011.582945

Dzhelyova, M., Jacques, C., & Rossion, B. (2017). At a single glance: Fast periodic visual stimulation uncovers the spatio-temporal dynamics of brief facial expression changes in the human brain. Cerebral Cortex, 27(8), 4106–4123. https://doi.org/10.1093/cercor/bhw223

Errante, A., Rossi Sebastiano, A., Ziccarelli, S., Bruno, V., Rozzi, S., Pia, L., Fogassi, L., & Garbarini, F. (2022). Structural connectivity associated with the sense of body ownership: a diffusion tensor imaging and disconnection study in patients with bodily awareness disorder. Brain Communications, 4(1), 1–15. https://doi.org/10.1093/braincomms/fcac032

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012a). A sensorimotor network for the bodily self. Journal of Cognitive Neuroscience, 24(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Ferri, F., Frassinetti, F., Ardizzi, M., Costantini, M., & Gallese, V. (2012b). A sensorimotor network for the bodily self. Journal of Cognitive Neuroscience, 24(7), 1584–1595. https://doi.org/10.1162/jocn_a_00230

Frassinetti, F., Ferri, F., Maini, M., Benassi, M. G., & Gallese, V. (2011). Bodily self: An implicit knowledge of what is explicitly unknown. Experimental Brain Research, 212(1), 153–160. https://doi.org/10.1007/s00221-011-2708-x

Frassinetti, F., Maini, M., Benassi, M., Avanzi, S., Cantagallo, A., & Farnè, A. (2010). Selective impairment of self body-parts processing in right brain-damaged patients. Cortex, 46(3), 322–328. https://doi.org/10.1016/j.cortex.2009.03.015

Frassinetti, F., Maini, M., Romualdi, S., Galante, E., & Avanzi, S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. Journal of Cognitive Neuroscience, 20(8), 1507–1516. https://doi.org/10.1162/jocn.2008.20067

Frassinetti, F., Pavani, F., Zamagni, E., Fusaroli, G., Vescovi, M., Benassi, M., Avanzi, S., & Farnè, A. (2009). Visual processing of moving and static self body-parts. Neuropsychologia, 47(8–9), 1988–1993. https://doi.org/10.1016/j.neuropsychologia.2009.03.012

Galvez-Pol, A., Calvo-Merino, B., Capilla, A., & Forster, B. (2018). Persistent recruitment of somatosensory cortex during active maintenance of hand images in working memory. NeuroImage, 174(February), 153–163. https://doi.org/10.1016/j.neuroimage.2018.03.024

Galvez-Pol, A., Calvo-Merino, B., & Forster, B. (2020). Revealing the body in the brain: An ERP method to examine sensorimotor activity during visual perception of body-related information. Cortex, 125, 332–344. https://doi.org/10.1016/j.cortex.2020.01.017

Hodzic, A., Muckli, L., Singer, W., & Stirn, A. (2009). Cortical responses to self and others. Human Brain Mapping, 30(3), 951–962. https://doi.org/10.1002/hbm.20558

Jeannerod, M. (2003). The mechanism of self-recognition in humans. Behavioural Brain Research, 142(1–2), 1–15. https://doi.org/10.1016/S0166-4328(02)00384-4

Kaplan, J. T., Aziz-Zadeh, L., Uddin, L. Q., & Iacoboni, M. (2008). The self across the senses: An fMRI study of self-face and self-voice recognition. Social Cognitive and Affective Neuroscience, 3(3), 218–223. https://doi.org/10.1093/scan/nsn014

Keyes, H., Brady, N., Reilly, R. B., & Foxe, J. J. (2010). My face or yours? Event-related potential correlates of self-face processing. Brain and Cognition, 72(2), 244–254. https://doi.org/10.1016/j.bandc.2009.09.006

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm. Human Brain Mapping, 36(6), 2284–2304. https://doi.org/10.1002/hbm.22770

Minnebusch, D. A., & Daum, I. (2009). Neuropsychological mechanisms of visual face and body perception. Neuroscience and Biobehavioral Reviews, 33(7), 1133–1144. https://doi.org/10.1016/j.neubiorev.2009.05.008

Morita, T., Saito, D. N., Ban, M., Shimada, K., Okamoto, Y., Kosaka, H., Okazawa, H., Asada, M., & Naito, E. (2017). Self-face recognition shares brain regions active during proprioceptive illusion in the right inferior fronto-parietal superior longitudinal fasciculus III network. Neuroscience, 348, 288–301. https://doi.org/10.1016/j.neuroscience.2017.02.031

Myers, A., & Sowden, P. T. (2008). Your hand or mine? The extrastriate body area. NeuroImage, 42(4), 1669–1677. https://doi.org/10.1016/j.neuroimage.2008.05.045

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereaur, B. R., & Rossion, B. (2015). The steady state VEP in research. Journal of Vision, 15(6), 1–46. https://doi.org/10.1167/15.6.4.doi

Pann, A., Bonnard, M., Felician, O., & Romaiguère, P. (2021). The Extrastriate Body Area and identity processing: An fMRI guided TMS study. Physiological Reports, 9(8), 1–14. https://doi.org/10.14814/phy2.14711

Pia, L., Fossataro, C., Burin, D., Bruno, V., Spinazzola, L., Gindri, P., Fotopoulou, K., Berti, A., & Garbarini, F. (2020). The anatomo-clinical picture of the pathological embodiment over someone else's body part after stroke. Cortex, 130, 203–219. https://doi.org/10.1016/j.cortex.2020.05.002

Platek, S. M., Wathne, K., Tierney, N. G., & Thomson, J. W. (2008). Neural correlates of self-face recognition: An effect-location meta-analysis. Brain Research, 1232, 173–184. https://doi.org/10.1016/j.brainres.2008.07.010

Rochat, P. (1989). Object Manipulation and Exploration in 2- to 5-Month-Old Infants. Developmental Psychology, 25(6), 871–884. https://doi.org/10.1037/0012-1649.25.6.871

Rochat, P., & Morgan, R. (1998). Two functional orientations of self-exploration in infancy. British Journal of Developmental Psychology, 16(2), 139-154.

Rochat, P., & Striano, T. (2000). Perceived self in infancy. Infant Behavior and Development, 23(3–4), 513–530. https://doi.org/10.1016/S0163-6383(01)00055-8

Ronga, I., Valentini, E., Mouraux, A., & Iannetti, G. D. (2013). Novelty is not enough: Laser-evoked potentials are determined by stimulus saliency, not absolute novelty. Journal of Neurophysiology, 109(3), 692–701. https://doi.org/10.1152/jn.00464.2012

Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. European Journal of Neuroscience, 52(10), 4283–4344. https://doi.org/10.1111/ejn.14865

Rubianes, M., Muñoz, F., Casado, P., Hernández-Gutiérrez, D., Jiménez-Ortega, L., Fondevila, S., Sánchez, J., Martínez-de-Quel, O., & Martín-Loeches, M. (2021). Am I the same person across my life span? An event-related brain potentials study of the temporal perspective in self-identity. Psychophysiology, 58(1), 1–14. https://doi.org/10.1111/psyp.13692

Saxe, R., Jamal, N., & Powell, L. (2006). My body or yours? The effect of visual perspective on cortical body representations. Cerebral Cortex, 16(2), 178–182. https://doi.org/10.1093/cercor/bhi095

Sel, A., Forster, B., & Calvo-Merino, B. (2014). The emotional homunculus: ERP evidence for independent somatosensory responses during facial emotional processing. Journal of Neuroscience, 34(9), 3263–3267. https://doi.org/10.1523/JNEUROSCI.0106-13.2014

Stapel, J. C., van Wijk, I., Bekkering, H., & Hunnius, S. (2017). Eighteen-month-old infants show distinct electrophysiological responses to their own faces. Developmental Science, 20(5). https://doi.org/10.1111/desc.12437

Sugiura, M. (2015). Three faces of self-face recognition : Potential for a multi-dimensional diagnostic tool. Neuroscience Research, 90, 56–64. https://doi.org/10.1016/j.neures.2014.10.002

Sugiura, M., Miyauchi, C. M., Kotozaki, Y., Akimoto, Y., Nozawa, T., Yomogida, Y., Hanawa, S., Yamamoto, Y., Sakuma, A., Nakagawa, S., & Kawashima, R. (2015). Neural mechanism for mirrored self-face recognition. Cerebral Cortex, 25(9), 2806–2814. https://doi.org/10.1093/cercor/bhu077

Sugiura, M., Sassa, Y., Jeong, H., Horie, K., Sato, S., & Kawashima, R. (2008). Face-specific and domain-general characteristics of cortical responses during self-recognition. NeuroImage, 42(1), 414–422. https://doi.org/10.1016/j.neuroimage.2008.03.054

Torta, D. M., Liang, M., Valentini, E., Mouraux, A., & Iannetti, G. D. (2012). Dishabituation of laser-evoked EEG responses: Dissecting the effect of certain and uncertain changes in stimulus spatial location. Experimental Brain Research, 218(3), 361–372. https://doi.org/10.1007/s00221-012-3019-6

Tsakiris, M. (2008). Looking for myself: Current multisensory input alters self-face recognition. PLoS ONE, 3(12), 2–7. https://doi.org/10.1371/journal.pone.0004040

Tugin, S., Hernandez-Pavon, J. C., Ilmoniemi, R. J., & Nikulin, V. V. (2016). Visual deviant stimuli produce mismatch responses in the amplitude dynamics of neuronal oscillations. NeuroImage, 142, 645–655. https://doi.org/10.1016/j.neuroimage.2016.07.024

Uddin, L. Q., Kaplan, J. T., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2005). Self-face recognition activates a frontoparietal “mirror” network in the right hemisphere: An event-related fMRI study. NeuroImage, 25(3), 926–935. https://doi.org/10.1016/j.neuroimage.2004.12.018

Vocks, S., Busch, M., Grönemeyer, D., Schulte, D., Herpertz, S., & Suchan, B. (2010). Differential neuronal responses to the self and others in the extrastriate body area and the fusiform body area. Cognitive, Affective and Behavioral Neuroscience, 10(3), 422–429. https://doi.org/10.3758/CABN.10.3.422

Von Hofsten, C., & Lindhagen, K. (1979). Observations on the development of reaching for moving objects. Journal of Experimental Child Psychology, 28(1), 158–173.

Zhang, R., Hu, Z., Debi, R., Zhang, L., Li, H., & Liu, Q. (2013). Neural processes underlying the “same”-"different" judgment of two simultaneously presented objects- An EEG study. PLoS ONE, 8(12). https://doi.org/10.1371/journal.pone.0081737

Zimmermann, F. G. S., Yan, X., & Rossion, B. (2019). An objective, sensitive and ecologically valid neural measure of rapid human individual face recognition. Royal Society Open Science, 6(6). https://doi.org/10.1098/rsos.181904