

Implicit self-other discrimination affects the interplay between multisensory affordances of mental representations of faces



David Zeugin^a, Norhan Arfa^a, Michael Notter^{a,b}, Micah M. Murray^{a,b,c,d}, Silvio Ionta^{a,c,e,*}

^a The Laboratory for Investigative Neurophysiology (The LINE), Department of Radiology and Department of Clinical Neurosciences, University Hospital Center and University of Lausanne, Lausanne, Switzerland

^b EEG Brain Mapping Core, Centre for Biomedical Imaging (CIBM), Lausanne, Geneva, Switzerland

^c Department of Ophthalmology, University of Lausanne, Jules-Gonin Eye Hospital, Lausanne, Switzerland

^d Department of Hearing and Speech Sciences, Vanderbilt University, Nashville, TN, USA

^e Rehabilitation Engineering Laboratory, Institute of Robotics and Intelligent Systems, Swiss Federal Institute of Technology (ETHZ), Zurich, Switzerland

ARTICLE INFO

Keywords:

Self-other discrimination
Mental rotation
Face inversion effect
Multisensory representations
Proprioception
Vision
Eyetracking

ABSTRACT

Face recognition is an apparently straightforward but, in fact, complex ability, encompassing the activation of at least visual and somatosensory representations. Understanding how identity shapes the interplay between these face-related affordances could clarify the mechanisms of self-other discrimination. To this aim, we exploited the so-called “face inversion effect” (FIE), a specific bias in the mental rotation of face images (of other people): with respect to inanimate objects, face images require longer time to be mentally rotated from the upside-down. Via the FIE, which suggests the activation of somatosensory mechanisms, we assessed identity-related changes in the interplay between visual and somatosensory affordances between self- and other-face representations. Methodologically, to avoid the potential interference of the somatosensory feedback associated with musculoskeletal movements, we introduced the tracking of gaze direction to record participants’ response. Response times from twenty healthy participants showed the larger FIE for self- than other-faces, suggesting that the impact of somatosensory affordances on mental representation of faces varies according to identity. The present study lays the foundations of a quantifiable method to implicitly assess self-other discrimination, with possible translational benefits for early diagnosis of face processing disturbances (e.g. prosopagnosia), and for neurophysiological studies on self-other discrimination in ethological settings.

1. Introduction

Self-other discrimination for faces is not limited to only visual perception. In fact it is influenced also by other perceptual modalities, including somatosensation [1]. Thus, by comparing visual and somatosensory percepts (as well as motor) with internal representations of self and other faces, we become able to recognize ourselves in a mirror and distinguish our face from another person’s one. At the representational level, the specificity of the relative weight between visual and somatosensory aspects of mental representations of faces is highlighted by the so-called “face inversion effect” (FIE). According to the FIE, upside-down images of faces are more difficult (and slower) to be mentally rotated to upright, with respect to images of inanimate objects [2]. On this basis, the FIE can be mechanistically considered a sign of a heavier weight of somatosensory (than visual) components of mental representations, while its absence (as for inanimate objects) suggests the activation of mainly visuo-spatial processing [3]. This difference

would put the fundamentals for a semantic distinction between mental representations of faces versus inanimate objects.

In the same vein, faces and inanimate objects might be only two entries of a continuum along which progressively more salient somatosensory affordances are attributed to different items. At which stage of this continuum does the FIE appear? Does it differentially affect images of faces with similar pictorial configuration but different details? Can identity-related distinctions be sufficient to trigger differences in the FIE? To answer these questions, it can be hypothesized that mainly visual affordances might be attributed to inanimate objects (more different with respect to the human body) and mainly somatosensory affordances might characterize the mental representation of faces (more similar to the human body). Thus, as the relative weight of visual and somato-vestibular affordances might change according to the characteristics of the entry within the continuum, we predicted that the more the entry is similar to oneself, the larger the impact of somatosensory affordances.

* Corresponding author at: CHUV – Nestle Hospital, Avenue Pierre Decker 5, 1011 Lausanne, Switzerland.
E-mail address: ionta.silvio@gmail.com (S. Ionta).

As the somatosensory impact can be accessed through the FIE, the magnitude of the FIE itself for different entries can be considered an objective measure of implicit self-other discrimination. For these reasons, in the present study we manipulated the identity of images of faces and measured the FIE in healthy participants. In particular, healthy participants indicated which eye (left, right) was covered by a black patch (mental rotation) in series of different face images (self, other) presented in four orientations (0° , 90° , 180° , 270°).

2. Material and methods

2.1. Participants

Twenty participants (male; mean age = 24.2 y.o. SD = 6.27) had at least an undergraduate education, were right-handed [4], and had normal vision and no neurological disease. The local Ethics Committee approved the study and participants read and signed an informed consent form prior the experiment, which was conducted in accordance with the Declaration of Helsinki 1964.

2.2. Stimuli and setup

Participants sat on a chair in front of a computer screen. They were presented with images of faces, one at a time, covering a visual angle of about 13° at a distance of 60 cm (Fig. 1A). Each image represented a real face without hair and ears. To manipulate identity, the images could represent either the participant himself (self-face), or a complete stranger (other-face). To exclude the potential influence of familiarity, the other-face image was an avatar image and was the same for all the participants. Images appeared centered on the computer screen, once at time, aligned straight in front of the participant, in one of four orientations (upright = 0° , 90° , 180° , 270°). On each image, one eye was covered by a black patch (Fig. 1A). The luminance of the difference images was equalized using an automated in-house software. The spatial features were equalized by programming that the tip of the nose of each image will be aligned with the centre of the screen.

2.3. Procedure

To show that implicit self-other discrimination is associated with a change in the relative weight of visual and somatosensory affordances of mental representation of faces, we recorded response times and accuracy while participants performed mental rotation of self- and other-face images. According to the mental rotation procedure [3], for each image, participants were asked to identify which eye was covered by the black patch (left or right). As the main question regarded implicit self-other discrimination, participants were not asked to explicitly recognize the identity of the presented images. The experimental session consisted of two runs, counterbalanced across participants. Each runs contained 48 images belonging to one identity (self, other). Each image was repeated three times at a given orientation, with the same image never presented twice in sequence [5]. Each trial began with a fixation cross in the centre of the computer screen followed by an Image

1000 ms later. Each image remained visible until a response was given [6]. Participants' gaze was continuously monitored and tracked (Eye-link 1000 eyetracking system). To avoid any possible influence of musculoskeletal movements and the associated proprioceptive changes on the task, participants indicated their responses by placing their gaze (staring at) to specific regions of the screen, i.e. they responded by staring at the regions marked as response "buttons" (frames including the words "left" or "right"). These "buttons" were positioned above and below the target image, in counterbalanced order across participants (Fig. 1). The eye-tracking system recognized where on the screen the participants were staring and, when they stared at one of the two "buttons", it encoded their responses as "left" or "right", accordingly. Therefore, RTs were defined as the time between the image onset and the stable positioning of the participant's gaze in one of the two "buttons".

2.4. Data preprocessing

Trials with RTs < 500 ms or > 3500 ms and incorrect trials were excluded from analysis [7–11], with a total loss of 8.6%. The RTs of the remaining (correct) trials were analyzed by means of a repeated measures analysis of variance (ANOVA), with identity (self-face, other-face), laterality (left-eye, right-eye), and orientation (0° , 90° , 180° , 270°) as within-subject factors. Post-hoc analyses were carried out using the Newman-Keuls test ($p < 0.05$).

3. Results

The analysis of variance (ANOVA) for response times (RTs) of correct responses, with identity (self-face, other-face), laterality (left-eye, right-eye), and orientation (0° , 90° , 180° , 270°) as main factors, showed the significant interaction between identity and orientation [$F(3,57) = 7.021$; $p < 0.01$]. Thus the FIE (RTs difference between images presented at 180° and 0°) was larger for self-face (418.1 ms) than other-face (183.3 ms) images (Fig. 1B). These differences between self- and other-face cannot be the result of image familiarity, as no main effect of identity was observed [$F(1,19) = 1.133$; $p = 0.301$].

The origin of the larger FIE for self-face images was explicated by the significant interaction between identity and orientation [$F(3,57) = 7.021$; $p < 0.01$]. The post-hoc comparisons of this interaction showed that for both self- and other-face images RTs increase from 0° (1041.7 and 1164.1 ms, respectively) to 180° (1459.8 ms and 1329.7 ms, respectively) (all $p < 0.01$) (Fig. 1C). These data suggest that the typical increase of RTs as a function of orientation was present for both kinds of images. The direct comparison between self and other-face images presented at the same orientation showed that at 0° the RTs for self-face (1041.7 ms) were significantly faster than other-face (1164.1 ms). By contrast, at 180° RTs for self-face (1459.8 ms) were significantly slower than other-face images (1329.7 ms) (all $p < 0.05$). This supports that the FIE (RTs difference between images presented at 0° and 180°) was larger for self- than other-face images.

Other significant effects generally confirmed previous studies on mental rotation [12–15]. In particular, there was a significant

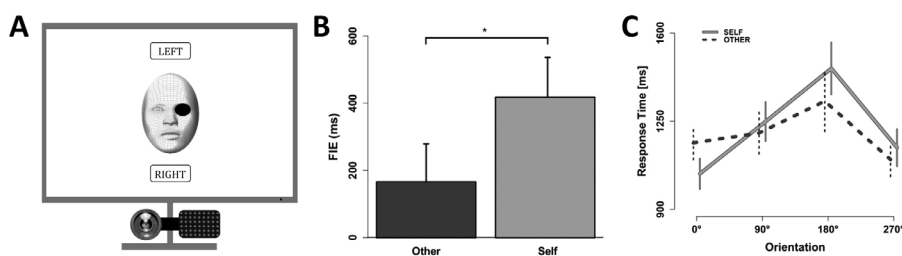


Fig. 1. A) Illustration of the experimental setup. The self- and other-face realistic images (represented here by an avatar face) were presented on a computer screen between two frames comprising the writings "left" and "right" ("response buttons"). An eye-tracking system positioned below the screen, detected where participants were looking during the whole experiment. Participants provided responses by staring at one of the two "buttons". B) Face Inversion Effect. The RTs difference between images presented at 180° and 0° was larger for self-face (grey) than other-face images (black). Error bars represent the confidence interval. The asterisk represents statistically significant difference. C) Kinesthetic aspects of face representation. Images' orientation had a larger impact on participants' performance (modulation of RTs) with self-face (grey-full line) than other-face images (black-dash line). Error bars represent the confidence interval. Asterisks represent significant differences between self- and other-faces, for each orientation.

interaction between Laterality and Orientation [$F(3;57) = 7.956$; $p < 0.01$], explained by images presented at 180° , where the responses for left-lateralized images (1463.6 ms) was slower than right-lateralized images (1325.8 ms; $p < 0.05$). Conversely, for images presented at 270° , responses for left-lateralized images (1050.5 ms) were faster than for right-lateralized images (1192.7 ms; $p < 0.05$). In addition, for other-face images, only the RTs for images presented at 180° were significantly slower with respect to all the other orientations (all $p < 0.05$). No significant identity-related differences were found for the 90° and 270° orientations, suggesting that only in the more common view (0°) and the most difficult view (180°) the representations of self- and other-face were differentially processed.

4. Discussion

In the present study we used the FIE as a quantitative method to assess implicit self-other discrimination for face images, based on the impact of somatosensory affordances onto mental representations of face. Our data provide evidence that implicit self-other discrimination is dependent not only on vision, but also on the changeable weight of constant somatosensation on face representation. Via the FIE we assessed that identity-related processing affects this relative weight of somatosensory affordances, in that it is greater for mental representation of self than other faces.

4.1. Visuo-somatosensory interplay for self-other discrimination

In normal conditions, people are faster to recognize their own face with respect to strangers' [16,17] and family members' faces [18], even if faces are upside-down [19]. Extending this evidence, the present study shows that, not only visual perception, but also mental representation of faces is affected by identity. The larger FIE for self-face images suggests that face-related somatosensory affordances have a greater weight on mental representation of self- than other-face. Such effect is considered a sign that the current body configuration is used as a frame of reference [3] and that physical constraints shape the mental representation of the body within this frame [20]. On this basis, we propose that the major role of somatosensory components could be emerging from the biomechanical constraints of the neck and head, leading to a specific impact on mental representation of self-face.

Combining visual and somatosensory input, we create a mental representation of our face, we identify it as belonging to ourselves, and we mentally process it in a different way with respect to another person's. Face-related multisensory inputs are usually matched in daily experience of self-face (grooming, shaving, applying make-up, etc.). Conversely, in the present study, the mismatch between the participants' face somatosensation (upright) and the presented face image (upside-down), may have disturbed more strongly the mental processing of self-face (than other-face), leading to the observed larger FIE. Considering that FIE is absent in young children [21], it is likely that the ability to distinguish identity is a learned process based on visual experience of faces. In this vein, as we are used to see (vision) and feel (somatosensation) our own face mainly upright, it is plausible that the larger FIE is due to a more crystallized (upright) representation of self-face, as the result of generally lacking experience in other orientations.

Where does the FIE come from? A larger orientation-dependent bias (difference between upright versus upside-down images) for self-faces than other-faces has been repeatedly reported both at the behavioral [17,19] and the brain level [22–24]. This identity-and-orientation effect is largely depending on the visual characteristics of the images because, for instance, it is absent in case of stretched faces [16]. Not only does upside-down inversion affect more self- than other-faces' processing, but also it suggests that upright and upside-down orientations could be only two extremes of a continuum. Accordingly, previous work reported that RTs progressively increase as a function of the angular disparity between the presented face image and the upright

position [3,25]. The present data are in line with this previous evidence, confirming the influence of orientation of mental processing of faces, and further extend previous results by showing that this influence is even larger for self- than other-faces.

4.2. Self- vs. other-face cognitive processing

Typically, self-other discrimination for faces is accomplished through (i) a comparison of the seen face with an average face representation, using the deviance from the average to attribute identity [26], or (ii) a holistic recognition based on configurational representation process, where parts of the face are analyzed and gathered independently [27]. In this perspective, we propose that self-face representation is treated as a holistic recognition process, including not only visual aspects, but also somatosensory ones. Conversely, as other-face representation depends less on somatosensation, it could be treated according to a comparison process. On this basis, we propose that we use internal holistic representations of our own face as a frame of reference to mentally transform and recognize self-face images.

The differentiation between self- and other-face mental representations is in line with the importance of and the distinction between “effector-based” versus “perspective” mental spatial transformations [28]. With respect to a fixed environment, effector-based transformations change the effector's coordinates (e.g. body parts), while perspective transformations change the participant's point of view. Thus, effector-based transformations would rely more on somatosensory representations, while perspective transformations would activate more visuo-spatial representations. In the present study, the larger FIE for self-face suggests the involvement of effector-based transformations, relying on somatosensory mechanisms. The smaller FIE for other-face suggests the prioritization of perspective transformations relying on visuo-spatial representations. We propose that the FIE is larger for self-face processing because the contrast between the actual somatosensory (upright) and visual input (upside-down) has a greater weight on the mental representations of self-face than other-face.

4.3. Perspectives and applications

The ability to attribute perceptions and actions to oneself or someone else is an index of self-consciousness across living species, from birds to humans [29]. Testing such self-other discrimination typically involves the mirror test: marking the subject's face and then presenting the subject with a mirror [30,31]. Although most self-aware species will probe this mark, many implementations of the mirror test have produced controversial data, including important limitations associated with cultural background, methodological procedures, and data interpretation [32]. Here, we introduce a novel index of implicit self-other discrimination in humans that capitalizes on the known FIE. As a sign of the involvement of somatosensory components in the mental representations of faces, the FIE entails longer behavioral responses to inverted than upright faces (of others) that is diminished, if not absent, for inanimate objects [2]. Here, we show that the FIE is more than doubled when viewing one's own face than another's.

These data provide a quantifiable test of the integrity of implicit self-other discrimination that can be applied in clinical and neuroethological settings alike. Considering the ease of the experimental procedures used here, the self-other discrimination method we introduce here can have important translational benefits. The implementation of the present setup and task in clinical and experimental environments can produce relevant advances for e.g. early diagnosis of clinical conditions affecting face processing (e.g. prosopagnosia) [33] or sensorimotor control (e.g. spinal cord injury) [15], as well as for neurophysiological research on self-representation in animal models [34] and the development of biomedical engineering solution for patients with reduced or absent mobility [35,36]. On this basis, future

studies will be required to identify the neurophysiological counterparts and brain activation patterns encoding such self-other discrimination at the representational level.

Funding sources

This work was supported by the Swiss National Science Foundation (grant PP00P1_170506 to S.I. and grant 320030_149982 to M.M.), the International Foundation for Research in Paraplegia (IRP; grant P64 to S.I.), and Carigest to M.M. The experimental procedures were independent from the funding source. All authors confirm no known conflict of interest.

Acknowledgments

The study was conceived by S.I., with input from M.M. The experimental setup and procedures were prepared by D.Z., N.A., and M.N., with input from S.I. The data were collected by D.Z., and N.A., under the supervision of S.I. The statistical analyses were conducted by D.Z. and N.A., under the supervision of S.I. The figures were created by D.Z., under the supervision of S.I. The paper was written by D.Z. and S.I., with input from M.M. All authors reviewed the manuscript.

References

- [1] M. Tsakiris, Looking for myself: current multisensory input alters self-face recognition, *PLoS One* 3 (12) (2008) e4040.
- [2] R.K. Yin, Looking at upside-down faces, *J. Exp. Psychol.* 81 (1) (1969) 141.
- [3] S. Ionta, A.D. Fourkas, S.M. Aglioti, Egocentric and object-based transformations in the laterality judgement of human and animal faces and of non-corporeal objects, *Behav. Brain Res.* 207 (2) (2010) 452–457.
- [4] R.C. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory, *Neuropsychologia* 9 (1) (1971) 97–113.
- [5] D. Perruchoud, L. Michels, M. Piccirelli, R. Gassert, S. Ionta, Differential neural encoding of sensorimotor and visual body representations, *Sci. Rep.* 6 (2016) 37259.
- [6] S. Ionta, A.D. Fourkas, M. Fiorio, S.M. Aglioti, The influence of hands posture on mental rotation of hands and feet, *Exp. Brain Res.* 183 (1) (2007) 1–7.
- [7] K. Sekiyama, Kinesthetic aspects of mental representations in the identification of left and right hands, *Percept. Psychophys.* 32 (2) (1982) 89–95.
- [8] L.A. Cooper, R.N. Shepard, Mental transformations in the identification of left and right hands, *J. Exp. Psychol. Hum. Percept. Perform.* 104 (1) (1975) 48–56.
- [9] M. Heil, B. Rolke, Toward a chronopsychophysiology of mental rotation, *Psychophysiology* 39 (4) (2002) 414–422.
- [10] Y. Steggemann, K. Engbert, M. Weigelt, Selective effects of motor expertise in mental body rotation tasks: comparing object-based and perspective transformations, *Brain Cogn.* 76 (1) (2011) 97–105.
- [11] S. Ionta, O. Blanke, Differential influence of hands posture on mental rotation of hands and feet in left and right handers, *Exp. Brain Res.* 195 (2) (2009) 207–217.
- [12] M. Fiorio, M. Tinazzi, S. Ionta, A. Fiaschi, G. Moretto, M.J. Edwards, K.P. Bhatia, S.M. Aglioti, Mental rotation of body parts and non-corporeal objects in patients with idiopathic cervical dystonia, *Neuropsychologia* 45 (10) (2007) 2346–2354.
- [13] S. Ionta, D. Perruchoud, B. Draganski, O. Blanke, Body context and posture affect mental imagery of hands, *PLoS One* 7 (3) (2012) e34382.
- [14] S. Ionta, A. Sforza, M. Funato, O. Blanke, Anatomically plausible illusory posture affects mental rotation of body parts, *Cogn. Affect. Behav. Neurosci.* 13 (1) (2013) 197–209.
- [15] S. Ionta, M. Villiger, C.R. Jutzeler, P. Freund, A. Curt, R. Gassert, Spinal cord injury affects the interplay between visual and sensorimotor representations of the body, *Sci. Rep.* 6 (2016) 20144.
- [16] J.P. Keenan, B. McCutcheon, S. Freund, G.G. Gallup, G. Sanders, A. Pascual-Leone, Left hand advantage in a self-face recognition task, *Neuropsychologia* 37 (12) (1999) 1421–1425.
- [17] M. Martini, I. Bufalari, M.A. Stazi, S.M. Aglioti, Is That Me or My Twin? Lack of self-face recognition advantage in identical twins, *PLoS One* 10 (4) (2015) e0120900.
- [18] M. Sugiura, Y. Sassa, H. Jeong, K. Horie, S. Sato, R. Kawashima, Face-specific and domain-general characteristics of cortical responses during self-recognition, *Neuroimage* 42 (1) (2008) 414–422.
- [19] H. Keyes, N. Brady, Self-face recognition is characterized by bilateral gain and by faster, more accurate performance which persists when faces are inverted, *Q. J. Exp. Psychol.* 63 (5) (2010) 840–847.
- [20] G. Vannuscors, A. Caramazza, Typical biomechanical bias in the perception of congenitally absent hands, *Cortex* 67 (2015) 147–150.
- [21] S. Carey, Becoming a face expert, *Philos. Trans. R Soc. Lond. B Biol. Sci.* 335 (1273) (1992) 95–102 discussion 102–3.
- [22] B. Rossion, I. Gauthier, M.J. Tarr, P. Despland, R. Bruyer, S. Linotte, M. Crommelinck, The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: an electrophysiological account of face-specific processes in the human brain, *Neuroreport* 11 (1) (2000) 69–72.
- [23] E. Eimer, Effects of face inversion on the structural encoding and recognition of faces: evidence from event-related brain potentials, *Cognit. Brain Res.* 10 (1) (2000) 145–158.
- [24] J.V. Haxby, L.G. Ungerleider, V.P. Clark, J.L. Schouten, E.A. Hoffman, A. Martin, The effect of face inversion on activity in human neural systems for face and object perception, *Neuron* 22 (1) (1999) 189–199.
- [25] T. Valentine, B. Bruce, Mental rotation of faces, *Mem. Cognit.* 16 (6) (1988) 556–566.
- [26] N. Kanwisher, J. McDermott, M.M. Chun, The fusiform face area: a module in human extrastriate cortex specialized for face perception, *J. Neurosci.* 17 (11) (1997) 4302–4311.
- [27] G. Loffler, G. Yourganov, F. Wilkinson, H.R. Wilson, fMRI evidence for the neural representation of faces, *Nat. Neurosci.* 8 (10) (2005) 1386–1391.
- [28] J.M. Zacks, P. Michelon, Transformations of visuospatial images, *Behav. Cogn. Neurosci. Rev.* 4 (2) (2005) 96–118.
- [29] M. Gross, Elements of consciousness in animals, *Curr. Biol.* 23 (22) (2013) 981–983.
- [30] G.G. Gallup, Chimpanzees: self-recognition, *Science* 167 (1970) 86–87.
- [31] G.G. Gallup Jr., S.M. Platek, K.N. Spaulding, The nature of visual self-recognition revisited, *Trends Cogn. Sci.* 18 (2) (2014) 57–58.
- [32] T. Suddendorf, D.L. Butler, The nature of visual self-recognition, *Trends Cogn. Sci.* 17 (3) (2013) 121–127.
- [33] M.J. Farah, K.D. Wilson, H.M. Drain, J.R. Tanaka, The inverted face inversion effect in prosopagnosia: evidence for mandatory, face-specific perceptual mechanisms, *Vision Res.* 35 (14) (1995) 2089–2093.
- [34] D.A. Leopold, I.V. Bondar, M.A. Giese, Norm-based face encoding by single neurons in the monkey inferotemporal cortex, *Nature* 442 (7102) (2006) 572–575.
- [35] I. Pisotta, D. Perruchoud, S. Ionta, Hand-in-hand advances in biomedical engineering and sensorimotor restoration, *J. Neurosci. Methods* 246 (2015) 22–29.
- [36] D. Perruchoud, I. Pisotta, S. Carda, M.M. Murray, S. Ionta, Biomimetic rehabilitation engineering: the importance of somatosensory feedback for brain-machine interfaces, *J. Neural Eng.* 13 (4) (2016) 041001.