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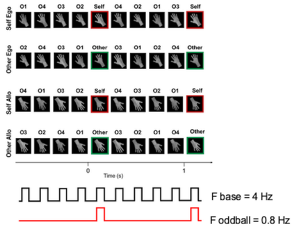
? Which are the neural mechanisms supporting categorical discrimination of visual self-identity?

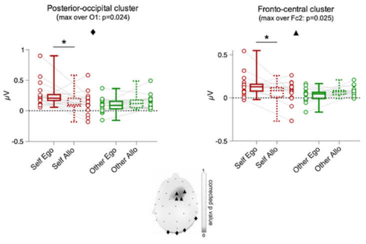
Electroencephalography

Fast Periodic Visual Stimulation



Does oddball frequency response vary with hand identity (self vs other) and perspective (egocentric vs allocentric)?

Identity * Perspective Interactiion



We observe greater responses for the self-hand in egocentric perspective in both occipital and fronto-central clusters

Spontaneous categorical discrimination of visual self-identity likely relies on the automatic association between visual and sensorimotor representations of the bodily self

Frequency-tagging EEG reveals spontaneous categorical discrimination of visual self-identity

Mattia Galigani[1], Nicolò Castellani[1,2], Barbara Italia[1], Sveva D'Aversa[1], Davide Bottari[2], Francesca Garbarini[1,3*].

1. MANIBUS Lab, Department of Psychology, University of Turin, Via Verdi 10, 10124, Turin, Italy

2. MoMiLab, IMT School for Advanced Studies Lucca, Piazza S. Ponziano, 55100, Lucca, Italy

3. Neuroscience Institute of Turin (NIT), Regione Gonzole 10, 10043, Orbassano, Italy

* Lead contact: francesca.garbarini@unito.it

SUMMARY

From early development, visual and sensorimotor representations of our hands are continually linked, allowing to develop a bodily self-representation. Here, we investigated the neural mechanisms of bodily self-identity discrimination, combining electroencephalography with fast periodic visual stimulation. In two experiments, participants' self-hand images appeared as oddball stimuli among others' hands. To control for statistical regularity and familiarity, oddball hand images could belong to a stranger (Exp1) or the partner (Exp2). In a third behavioral experiment, we verified participants could explicitly detect the presence of the self-hand in the sequence. Results revealed a neural marker for automatic hand identity discrimination, with greater responses in egocentric than allocentric perspective only for self-hand images. This interaction effect emerged over occipital, consistently with the visual nature of the task, but also over fronto-central regions, compatibly with the involvement of a sensorimotor network. These findings support that self-hand processing relies on associating visual and sensorimotor representations.

Keywords

EEG, Fast Periodic Visual Stimulation, Frequency Tagging, Visual self-identity, body representation

INTRODUCTION

Our hands represent multifaceted devices capable of a wide variety of functions, serving as a vital interface between individuals and their environment. From a phylogenetical perspective, hands are a distinguishing feature of humans primates and played an evolutionary role in shaping cognitive, emotional, and linguistic development [1]. From an ontogenetic point of view, hands might represent one of the earliest opportunities to distinguish our bodies from others' bodies, as a result of the uniqueness of the multisensory experience involving our hands. Indeed, while using our hands to interact with objects and other people, we have a continuous access from a first-person (egocentric) perspective to the hands visual features that are constantly associated with tactile and proprioceptive inputs [2–8]. This convergence of multisensory signals may be fundamental in developing a coherent sense of bodily-self because only the hand on which multisensory signals converge is *mine* [9,10]. However, the neural mechanisms of bodily self-identity have been mainly investigated by focusing on the face, given the role of facial cues in discriminating a person's identity, even in absence of a direct visual access to them [11–14]. In the present study, we focused on the hands as a neglected yet fundamental line of research for understanding the neural mechanisms subserving visual self-identity.

To characterize the brain dynamics underlying spontaneous categorical processing of our hands identity, we combined electroencephalography (EEG) with 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., 4 Hz) elicits an electrical brain activity precisely at the stimulation rate (i.e., 4 Hz), measured with EEG [15]. While FPVS has been traditionally confined to the study of low-level visual processes [16,17], in more recent years, it has been extended to assess visual discrimination of more complex images [18–21] and provided sensitive measures of the processing of body parts [22–24].

In two experiments (Fig.1), we designed an oddball version of FPVS that consisted in repeating hand images belonging to the same “non-self” category (i.e., other people’s hands) at a rapid frequency rate (base frequency: 4 Hz) and introducing, every five stimuli, a categorical change by presenting the participant’s hand image (self-hand). This generated a specific periodic frequency of stimulation associated with self-hand (oddball frequency: 4 Hz/5 = 0.8 Hz). In the case of a differentiation between base (someone else’s hands) and oddball (self-hand) stimuli, we expect brain activity to synchronize with the oddball frequency stimulation. This response would represent a neural index of the categorical discrimination of hand identity. This index was expected to be modulated by the identity of the hand displayed as oddball stimulus that, in the main condition explained above, could belong to the participant (self-hand) while, in control conditions of Experiment 1 and Experiment 2 respectively, to a randomly selected stranger (other-hand) or to the partner (familiar-hand). Furthermore, since the hand identity discrimination was expected to interact with the canonical hand orientation, we also manipulated the hand perspective by displaying hand images in either egocentric or allocentric perspective. We anticipated larger responses to the oddball frequency when the self-hand was perceived in canonical (egocentric) perspective. The scalp map distribution of this expected interaction should reveal whether the effect is confined in occipital regions, due to the visual nature of the task, or is also spread to fronto-central regions, thus supporting the view that the self-hand categorical processing in egocentric perspective relies on the association between visual and sensorimotor representations.

Finally, in a third behavioral experiment, we employed the very same stimuli and stimulation frequency as in Experiment 1 and 2 to verify whether participants were able to explicitly detect the presence/absence of the self-hand in the stimulation sequence. If so, participants were expected to exhibit a high sensibility when asked to report whether their own hand was present or not.

RESULTS

Experiment 1

In Experiment 1, in a sample of eighteen healthy participants (13 women, mean age ± SD: 24.38 ±3.53), to investigate the neural dynamics supporting categorical processing of our hands identity, we periodically presented, as oddball stimuli (0.8 Hz) either the image of the self- or a constant other-hand, embedded in a stream of images strangers' hands (4 Hz). Stimuli were presented in egocentric or allocentric perspective in different blocks, thus yielding four different conditions according to the identity and orientation of the oddball stimuli (Self Ego, Self Allo, Other Ego, Other Allo).

Oddball frequency

Our paradigm was able to unveil a neural index of categorical discrimination of hand identity, as revealed by the clear presence of tagged responses at the periodic rate in the stimulation frequency corresponding to the hand identity change. In particular, the stimulation rate of 0.8 Hz generated a significant ($z>1.64$; $p<0.05$) response at the oddball frequency at the first nine consecutive harmonics (i.e., 0.8 Hz, 1.6 Hz, 2.4 Hz and so forth – excluding the 4 Hz harmonic) (Fig.2-4).

Then, we performed statistical analysis (2x2 design corrected with 1000 permutation to account for multiple comparisons problem) to investigate whether this categorical discrimination index was modulated by the hand identity of the oddball stimulus that could represents either the hand belonging to the participant (self-hand) or to the same stranger (other-hand), by the perspective of the presented hand image that could be either egocentric or allocentric, or by their interaction. Our results did not show over any electrode a significant Main Effect of Perspective (p always > 0.125), thus not revealing any overall preference for one of the two perspectives, but showed a significant Main Effect of Identity with greater responses to the self-hand as compared to the other-hand over a fronto-central cluster (Fz, F4, Fc2; maximal over Fc2: p=0.029) and over a posterior-occipital cluster (POz, Oz, O2; maximal over O2: p=0.008) (Fig. 3A). Crucially, the hand identity discrimination was modulated by the canonical perspective of the hand image presentation, as revealed by the significant Identity*Perspective interaction over both a fronto-central (Fz, F4, FcZ, Fc2; maximal over Fc2, p=0.025) and a posterior-occipital cluster (P8, O1, Oz, O2; maximal over O1: p=0.024) (Fig. 3B). As revealed by post-hoc comparisons, such effect is driven by the self-hand eliciting greater responses when presented in egocentric (mainly consistent with looking at one's own body) than allocentric perspective (in each cluster maximal over F4, p=0.012, and maximal over P8, p=0.029), while no differences between perspectives is present when discriminating the other-hand (p*s* always > 0.092).

Base Frequency

The control analysis run over responses at the base frequency (i.e., 4, 8, and 12 Hz), did not reveal any significant effect (Main effect of Perspective: p*s* always > 0.067; Main effect of Identity: p*s* always > 0.143; Identity*Perspective interaction: p*s* always > 0.131). These results suggest that the brain responses common with all stimuli, which are a mixture of low- and high-level visual processes and is projected to the base rate (4 Hz) and its harmonics, did not differ between conditions, and cannot explain the results obtained analyzing oddball responses[23].

Experiment 2

In Experiment 2, in a sample of eighteen participants (different from those enrolled in Experiment 1; 13 women, mean age ± SD: 26.94 ± 3.81), we controlled for any familiarity effect driving our results of Experiment 1, and we periodically presented, as oddball stimuli (0.8 Hz) either the image of the self- or a famiiliar-hand, embedded in a stream of images strangers' hands (4 Hz). Stimuli were presented in egocentric or allocentric perspective in different blocks, thus yielding four different conditions according to the identity and orientation of the oddball stimuli (Self Ego, Self Allo, Fam Ego, Fam Allo).

Oddball frequency

As in Experiment 1, our paradigm was able to unveil a neural index of categorical discrimination of hand identity, with the stimulation rate of 0.8 Hz that generated a significant ($z>1.64$; $p<0.05$) response at the oddball frequencies across the first thirteen consecutive harmonics (i.e., 0.8 Hz, 1.6 Hz, 2.4 Hz and so forth – excluding the 4 Hz harmonic) (Fig.5-7).

The statistical analysis (2x2 design corrected with 1000 permutations) performed to investigate the modulation of oddball responses induced by hand identity, hand perspective and their interaction showed over any electrode neither a significant Main Effect of Perspective (p always > 0.147) nor a significant Main Effect of Identity (p*s* always > 0.062).

Crucially, as in Experiment 1, the identity-related visual discrimination was modulated by the canonical perspective of the hand presentation, as revealed by the significant Identity*Perspective interaction over both a fronto-central (F4, C4, Fc4, Fc6; maximal over F4, p=0.010) and a posterior-occipital cluster (P8, PO8, Oz, O2; maximal over P8: p=0.003) (Fig. 6). Post-hoc tests revealed that such effect is driven by the self-hand eliciting greater responses when presented in egocentric than allocentric perspective (in each cluster maximal over C4, p=0.002, and maximal over P8, p=0.003), while no differences between perspectives is present when discriminating the familiar-hand (p*s* always > 0.365).

Base Frequency

The control analysis run over responses at the base frequency (i.e., 4, 8, and 12 Hz), did not reveal any significant effect (Main effect of Perspective: p*s* always > 0.084; Main effect of Identity: p*s* always > 0.369; Identity*Perspective interaction: p*s* always > 0.545). These results suggest that the brain responses common with all stimuli, which is a mixture of low- and high-level visual processes and is projected to the base rate (4 Hz) and its harmonics did not differ between conditions and cannot explain the results obtained analyzing oddball responses.

Experiment 3

In Experiment 3, in a sample of seventeen participants (different from those enrolled in Experiment 1 and 2; 12 females, mean age ± SD: 27.36 ± 2.64), we adapted the paradigm used in the EEG experiments (dividing each condition in smaller blocks of 25 s) to obtain behavioral evidence about the explicit detection of the self-hand within the stimulation stream. After each block, participants were asked to indicate whether their own hand had been present in the sequence by providing a “yes/no” response. Using the proportions of hits and false alarms, we computed d’ as an index of sensitivity to the presence of one’s own hand, and criterion as a measure of response bias.

Crucially, across conditions, we observed consistently higher sensitivity values (average between conditions; d’: mean±SD= 2.68±1.91) and lower bias values (average between conditions; criterion: mean±SD= -0.29±0.41), indicating that participants were generally able to discriminate their own hand reliably and without adopting a strongly conservative or liberal response strategy (d′ > 2.5 is typically considered high sensitivity, while criterion values close to 0 indicate a neutral response bias; see Macmillan and Creelman, 2004) (Fig.8). This diametrical modulation of d’ and criterion (high d’ combined with near-zero criterion) suggests a genuine difference in perceptual sensitivity rather than a shift in decision criterion [25,26]. These findings confirm that the self-hand was explicitly detectable within the FPVS stimulation stream and support the interpretation that the EEG responses reflect identity-specific visual processing.

Furthermore, sensitivity was higher in the egocentric condition (mean±SD= 3.08±1.79) compared to the allocentric condition (mean±SD= 2.28±2.01), and a paired-samples t-test confirmed that this difference was statistically significant (t_{16}=2.401, p = 0.027). This indicates that participants were more able to discriminate their own hand when it was presented from a first-person perspective, paralleling EEG results that showed that self-identity visual discrimination is enhanced by the canonical perspective (i.e., egocentric) of the hand presentation. In contrast, the criterion values did not significantly differ between the two perspectives (t_{16}=0.755, p =0.461; ego: mean±SD= -0.32±0.40, allo: mean±SD= -0.25±0.42). This suggests that participants’ general tendency to respond “yes” or “no” (i.e., their response bias) was comparable across perspectives.

DISCUSSION

In the present study, we sought to investigate the brain mechanisms sustaining the categorical discrimination of bodily self-identity by combining EEG with FPVS technique. To this aim, we periodically presented the participant’s hand image (self-hand) as the oddball stimulus within a sequence of hand images belonging to other individuals as the base stimuli. In Experiment 1, to control for statistical regularity, we also presented as oddball stimulus a constant hand image belonging to the same individual (other-hand). In Experiment 2, to control for familiarity, we presented as oddball stimulus the image of the partner’s hand (familiar-hand). This presentation technique splits the neural response evoked by the identity of interest (oddball stimulus: self or other in Experiment 1 and self or familiar in Experiment 2) into a separate response frequency from that of base stimuli. 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 the brain specifically coded the periodic change of hand-identity in the stimulation stream. Thus, this method allows to obtain a neural index of categorical discrimination of hand identity. Finally, in Experiment 3, we controlled for the participants ability to explicitly discriminate the presence/absence of the self-hand in the stimulation sequence.

As a first remarkable result, we report the success of our FPVS protocol in eliciting the detection of the hand identity change when the image of the self-hand was periodically included in a sequence of hand images belonging to other individuals. In both EEG experiments, this change detection was objectively and statistically identified at the specific frequency rate of the oddball stimulus (i.e., 0.8 Hz and its harmonics), and such responses were highly consistent across participants (Fig.4-7 - top panels). Despite few studies previously employed FPVS protocol to investigate self-identity processing in the face domain [13,14,27], our results originally reveal that our brain is endowed with a fast and automatic mechanism to discriminate between different body identities also when identity information is conveyed by hand visual features. This neural discrimination is paralleled by explicit behavioral detection, as shown in Experiment 3, where participants accurately reported the presence of their own hand in the stimulation stream.

The comparison with the control condition of the Experiment 1 allows us to unveil the specificity of our paradigm in eliciting categorical discrimination mechanism. In Experiment 1, we controlled for the statistical regularity embedded in the paradigm. Indeed, oddball responses may be also elicited when our brain statistically detects the presence of regularity patterns in the stimulation stream [53].

Since here we aimed to investigate the neural mechanisms underlying the discrimination of the only hand that falls outside the category of non-self hands, we had to employ a single image as oddball stimulus (i.e., the self-hand image). This might have introduced some statistical regularity into the experiment, potentially influencing the emergence of oddball responses [53]. To address this concern, we included a control condition in which we presented a constant image of the other-hand as oddball stimulus. This allowed us to balance the statistical cues across conditions, ensuring that differences between conditions reflect actual processing of hands with distinct identities, rather than the detection of regularity patterns in the visual stimuli. Accordingly, the constant image of the other-hand also elicited oddball responses (Fig.4 - bottom panel); however, the amplitude of these responses was significantly higher in the self-hand condition, when the deviant stimulus implied a categorical change between two categories (self vs others) as compared to when it implied the detection of statistical regularities within the same category (constant other vs others). Coherently, in Experiment 2, this categorical discrimination mechanism was also elicited by familiar hands, when presenting as oddball stimulus the images of the partners' hands (Fig.7 – bottom panel). Indeed, we observed responses at the oddball frequency but, in this case, the overall magnitude did not differ from that elicited by the self-hand (Fig. 6), since both kind of stimuli induced a categorical change related to hand-identity (self vs others and familiar vs strangers).

The specificity of this categorical discrimination for the self-hand emerges from the interaction with the perspective of hand images presentation and the topography of this effect in the brain, showing highly consistent results between the two EEG experiments. Indeed, in both experiments, we found that the hand identity discrimination interacts with the hand orientation, with the self-hand image eliciting significantly larger responses at the oddball stimulation frequency when observed in canonical (egocentric), through which we usually see our own hand, than allocentric perspective. Thus, regardless of whether the comparison is made with the oddball response to the other-hand

(Experiment 1 – Fig. 3B) or to the familiar-hand (Experiment 2 – Fig 6), the peculiarity of the self-hand discrimination lies in this modulation of perspective and such mechanism is not driven by the familiarity of visual features. Again, this neural discrimination is paralleled by explicit behavioral recognition, as shown in Experiment 3, where participants were more accurate in reporting the presence of their own hand when presented in egocentric perspective. Overall, this perspective effect that emerges in our results is consistent with the idea that self-other distinction is strongly grounded in spatial reference frames [28–30]. This account emphasizing the role of perspective in body representation is supported by the broad literature about body ownership manipulations in healthy subjects [31,32] and brain-damaged patients [33] that showed that embodiment mechanism only occurs in first-person perspective, thus fitting with the egocentric representation of the own body. Alternatively, the visual parameters of the experimental stimuli used in our study (degraded visibility using grey-scale pictures) may have modulated identity-related visual activity [34–37]. Indeed, previous evidence showed that visual degradation promotes a shift from allocentric (visual) to egocentric (sensorimotor) strategies, and this may have facilitated the engagement of egocentric reference frames and embodiment-related processes [38]. In this light, it remains an open question whether using colored or more naturalistic hand images would maintain the egocentric preference observed here for the self-hand.

The topographical localization of the interaction effect reveals crucial aspects of the neural mechanism that supports self-hand discrimination. We found prominent responses to the self-hand in egocentric perspective over a posterior-occipital and a fronto-central cluster (Fig.4,7). The posterior distribution agrees the visual nature of the task and the scalp localization of hand-selective responses previously highlighted by electrophysiological [39], neuroimaging [40–42] and brain stimulation [43,44] studies. This scalp topography may suggest that these responses essentially originate from regions of the visual and extrastriate cortices, that have been demonstrated to be sensitive to images of our own or others' hands, thus revealing that they might perform an important sorting of body part images by identity [45]. Interestingly, the presence of a fronto-central cluster may unveil the involvement of sensorimotor regions in the self-hand discrimination. This sensorimotor contribution is compatible with the hypothesis of an integrated, multisensory network devoted to bodily-self representation [2,46–49]. Differently from images depicting others' bodies, of which we can have only a visual representation, 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 that are associated with the visual features of the self-hand in egocentric perspective. This supports the view that self-hand processing in the canonical (egocentric) perspective relies on the association between visual and sensorimotor representations, likely occurring during hand movements.

To sum up, in the present study, we characterized the neural dynamics subserving the categorical discrimination of bodily self-identity by focusing on the hand representation. We demonstrated that i) our brain is endowed with a fast and automatic mechanism to discriminate between different body identities also when identity information is provided by hand visual features; ii) the specificity of bodily self-identity emerges from the interaction with the hand orientation, with the self-hand image showing larger responses when perceived in canonical (egocentric) perspective; iii) the neural mechanism supporting the self-hand discrimination relies on the association between visual and sensorimotor representations. This paradigm, successfully applied in adults, has a high signal to noise ratio with a very short stimulus presentation, thus opening the way to explore self-hand identity discrimination as a proxy of bodily self-representation development early in life. Different from faces, the visual details of our hands (in egocentric perspective) are always available since our first movement attempts, and they are constantly associated with sensorimotor representations.

Thus, in developmental context, the hand may represent the key body part for experiencing the convergence of multisensory signals that, in turn, allows the emergence of a primitive bodily self-identity.

LIMITATIONS OF THE STUDY

Even though the present study provides compelling evidence for a neural marker of automatic hand identity discrimination, some limitations should be acknowledged. For instance, our study focused only on the neural mechanisms supporting the coding of the hand identity. Future applications of our protocol could establish whether the present findings can be generalized to other body-parts. Furthermore, although the topographical distribution of our effects supports the role of sensorimotor areas in coding visual self-hand identity, we recognize that EEG is not the method of choice for a precise spatial location of neural activations. Future studies could build upon our findings by employing neuroimaging techniques with higher spatial resolution, such as functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS), to obtain a more precise characterization of the neural substrates underlying visual self-hand identity processing.

AUTHOR CONTRIBUTION

Mattia Galigani: Conceptualization, Methodology, Data Collection, Data Analysis, Writing – Original Draft, Writing – Review & Editing; **Nicolò Castellani**: Data Collection, Writing – Review & Editing; **Barbara Italia**: Data Collection, Writing – Review & Editing; **Sveva D'Aversa**: Data collection; **Davide Bottari**: Conceptualization, Methodology, Data Analysis, Writing – Review & Editing; **Francesca Garbarini**: Conceptualization, Methodology, Supervision, Project administration, Writing – Original Draft, Writing – Review & Editing, Funding acquisition. All co-authors have read and approved the final version of the manuscript.

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DECLARATION OF INTERESTS

The authors declare no competing interest.

Figure titles and legends

Figure 1. Exp1, 2 - Experimental paradigm

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 four different strangers' hands (O1, O2, O3, and O4). Oddball stimuli, according to the experimental block, represented the self-hand image (Self) or a constant other-hand image (Other) (different from those used as base stimuli) in Experiment 1 (Panel A), and the self-hand image (Self) or a familiar-hand image (Fam) in Experiment 2 (Panel B). The same stimulation paradigm was used in the behavioral Experiment 3, where participants were asked to explicitly indicate after each block whether their own hand had been present by giving a "yes/no" response.

Figure 2. Exp 1 - SNR and topographical maps

Panel A represents grand-averaged SNR spectra across posterior-occipital cluster (averaged across channels O1, Oz, O2, P8) in the four different conditions. Note that the y-axis is cut between 2 and 8 µV to have a better visualization of the SNR of each oddball harmonic. Panel B depicts the topographical CSD maps of the baseline subtracted oddball responses in the four different conditions.

Figure 3. Exp 1 - Sum of oddball responses

Sum of oddball responses depicting the significant Main effect of Identity with its p-map are shown in panel A. The box spans from the first quartile (Q1) to the third quartile (Q3), with the line inside representing the median. The whiskers extend to the minimum and maximum values, and individual points are represented by circles. Triangles and rhombuses represent significant electrodes. Panel B represents the sum of oddball responses depicting the significant Identity*Perspective interaction Identity with its p-map. Asterisks represent significant differences.

Figure 4. Exp 1 - Individual responses across participants

In each subpanel, the left panels show the group-averaged responses obtained by summing baseline-subtracted chunks of significant harmonics at the oddball frequencies, computed separately for each of the four conditions and for two clusters: posterior-occipital (triangles) and fronto-central (rhombuses); error bars indicate SEM. The right panels show individual responses.

Figure 5. Exp2 - SNR and topographical maps

Panel A represents the grand-averaged SNR spectra across posterior-occipital cluster (averaged across channels Oz, O2, Po8, P8) in the four different conditions. Note that the y-axis is cut between 4 and 6 µV to have a better visualization of the SNR of each oddball harmonic. Panel B depicts the topographical CSD maps of the baseline subtracted oddball responses in the four different conditions.

Figure 6. Exp 2 - Sum of oddball responses

The figure represents the sum of oddball responses depicting the significant Identity*Perspective interaction Identity with its p-map. The box spans from the first quartile (Q1) to the third quartile (Q3), with the line inside representing the median. The whiskers extend to the minimum and maximum values, and individual points are represented by circles. Triangles and rhombuses represent significant electrodes. Asterisks represent significant differences.

Figure 7. Exp 2 - Individual responses across participants

In each subpanel, the left panels show the group-averaged responses obtained by summing baseline-subtracted chunks of significant harmonics at the oddball frequencies, computed separately for each of the four conditions and for two clusters: posterior-occipital (triangles) and fronto-central (rhombuses); error bars indicate SEM. The right panels show individual responses.

Figure 8. Exp 3 – Discrimination task

The figure represents the d' (left panel) and criterion (right panel) of the discrimination task, where participants were asked to indicate whether their own hand had been present in the sequence by providing a yes/no response. A. The box spans from the first quartile (Q1) to the third quartile (Q3), with the line inside representing the median. The whiskers extend to the minimum and maximum values, and individual points are represented by circles. Asterisks represent significant differences.

STAR METHODS

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Prof. Francesca Garbarini (francesca.garbarini@unito.it)

Materials availability

This study did not generate new materials.

Data and code availability

- De-identified data are deposited at Mendeley data and are publicly available as of the date of publication. DOI is listed in the key resources table.
- All original code for running the experiments reported in this paper are deposited at Mendeley data and are publicly available as of the date of publication. DOI is listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAIL

In Experiment 1, eighteen healthy right-handed subjects participated in the study (13 women) aged 20-27 years (mean±SD: 24.38 ± 3.53; years of education: 17 ±1.28). In Experiment 2, we recruited eighteen healthy right-handed subjects (different from those enrolled in Experiment 1) (13 women) aged 22-34 years (mean±SD: 26.94 ± 3.81; years of education: 17.61 ±0.70). Furthermore, 17 right-handed participants (12 females)aged 24-31 years took part to the behavioral Experiment 2 (mean age ± SD: 27.36 ± 2.64; years of education: 17.82 ± 0.39).

Sample size was estimated based on a previous study[59] using the following parameters: dz=0.91, alpha= 0.05, estimated power= 95% and using as dependent variables the amplitudes of oddball stimuli in the upright condition *vs* inverted condition.

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

METHODS DETAILS

Stimuli and experimental procedure

Visual stimuli consisted of grey-scale pictures (20x20cm) of the dorsum of open right hands belonging either to the participant (self-hand) or to someone else (Fig. 1). 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 black background. Then, we converted original color pictures in grey-scale images [50,51]. The resulting visual stimuli were presented at the center of a 24-inches Sony CRT computer screen (screen resolution of 1280 pixels x 1024 pixels at a refresh rate of 120 Hz).

Participants sat at a table in a dimly lit room in front of a computer monitor at a viewing distance of 55 cm. 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 an oddball stimulus was included every five images (0.8 Hz). Base stimuli consisted of four hand images belonging to four different strangers individuals (sex-matched). Their order was presented randomized. In Experiment 1, in different experimental conditions, the oddball stimulus might depict either the self-hand image or a constant hand image belonging to the same individual (other-hand), which was always different from hand images used as base stimuli that belonged to four different strangers individuals (Fig.1A). In this way, we controlled for statistical regularity by matching the frequency of occurrence of individual stimuli[53]. By using four different images as base stimuli and one image as the oddball stimulus, we ensured that the oddball stimulus and each base stimuli appeared with equal frequency (each stimulus was presented 60 times in every sequence), as in previous studies [52,54].

Visual stimuli were presented in egocentric or allocentric perspective, thus yielding four different conditions (Fig,1A):

1) Self Ego: the image of the self-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in egocentric perspective.

2) Other Ego: the image of an other-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in egocentric perspective.

3) Self Allo: the image of the self-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in allocentric perspective.

4) Other Allo: the image of an other-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in allocentric perspective.

In Experiment 2, instead of presenting the image of a stranger’s hand as an oddball stimulus, we presented a familiar stimulus to the participant: the image of the hand of the participant’s partner.

Note that, as inclusion criteria, participants had to been in a romantic relationship with the partner for at least three years and had to live in the same city. As in Experiment 1, base stimuli consisted of four hand images belonging to four different individuals (sex-matched). Thus, the experimental design consisted of four different conditions (Fig.1B):

1) Self Ego the image of the self-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in egocentric perspective.

2) Fam Ego: the image of a familiar-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in egocentric perspective.

3) Self Allo: the image of the self-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in allocentric perspective.

4) Fam Allo: the image of a familiar-hand as oddball stimulus and four different strangers hands as base stimuli. All stimuli presented in allocentric perspective.

In both experiments, the order of conditions was pseudo-randomized between subjects. 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, 7 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.

In Experiment 3, we adapted the paradigm used in the EEG experiments to obtain behavioral evidence about the explicit discrimination of the self-hand within the stimulation stream. This additional experiment was designed in response to concerns regarding the visual similarity of the stimuli and the brief presentation time, which may challenge the assumption that participants could reliably distinguish their own hand from other hands. By directly probing self-hand discrimination under conditions closely matching the EEG experiments, this behavioral validation allows us to empirically assess whether the observed neural responses indeed reflect explicit identity-specific processing.

The stimuli and stimulation procedure used in Experiment 3 were adapted from Experiment 1 and followed the same FPVS structure, with a base frequency of 4 Hz and an oddball stimulus occurring every fifth image (0.8 Hz). The four conditions (Self Ego, Other Ego, Self Allo, Other Allo) were identical to those in Experiment 1, using egocentric or allocentric perspectives and including either the self-hand or an other-hand as oddball stimuli, while base stimuli always consisted of four sex-matched strangers' hands. The main procedural difference was the block structure. Each condition was divided into 16 blocks lasting 25 seconds each. At the end of each block, participants were asked to indicate whether their own hand had been present in the sequence by providing a ‘yes/no’ response. This allowed the collection of behavioral data on self-hand detection under fast visual presentation conditions. The order of conditions was pseudo-randomized between subjects.

EEG Recording

In Experiment 1, 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. To replicate the findings of Experiment 1 and control for familiarity effects, in Experiment 2 we recorded the EEG with a more powerful system with 64 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 *BrainAmp DC* amplifier (Brain Products) and a 1,000 Hz sampling rate.

During the experiments, 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.

QUANTIFICATION AND STATISTICAL ANALYSIS

Frequency domain analysis

In Experiment 1 and 2*,* all EEG data were analyzed using the free software Letswave 6 [55], and MATLAB.

Pre-processing and analysis procedures, including the identification of significant harmonics and data normalization, were applied in accordance with the studies using FPVS paradigms [21,23,56–59]. Nonetheless, all steps are fully described here.

First, a Butterworth bandpass (fourth-order, 0.1–100 Hz cut-off) filters was applied to EEG raw data, which were down-sampled from 1024 to 512 Hz in Experiment 1 and from 1000 to 500 Hz in Experiment 2 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. Biological artifacts due to eye blinks or eye movements were eliminated using a validated method based on an Independent Component Analysis[61]. 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. 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 to avoid spectral leakage to the neighboring frequencies. Then, the recording sequences of each condition were concatenated. 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 $1/75=0.01\overline{3}$ Hz.

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 [57,58,60], 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 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 [23,62,63]. Z-scores were significant (i.e., $z>1.64$) until the ninth harmonic (i.e., until 8.8 Hz - excluding the 4 Hz 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) [16]. 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 (z-value larger than 1.64), were then combined into a summed response at the single participant level [23,59,62,63]. Once the summed oddball response was averaged for each participant, it was used as a dependent measure for further statistical analyses. To compare the amplitude of oddball responses across experimental conditions, we performed paired t-tests and a permutation-based correction. In particular, in Experiment 1, we recreated a 2*2 design by performing t-tests over each electrode between Self and Other conditions by averaging responses in egocentric and allocentric perspective (Main Effect of Identity), between Egocentric and Allocentric conditions by averaging responses to self and other identity (Main effect of Perspective), and between the differences within factor levels (i.e., Self Ego *minus* Self Allo vs Other Ego *minus* Other Allo: Identity*Perspective interaction). In

Experiment 2, we recreated a 2*2 design by performing t-tests over all electrodes between Self and Familiar conditions by averaging responses in egocentric and allocentric perspective (Main Effect of Identity), between Egocentric and Allocentric conditions by averaging responses to self and familiar identity (Main effect of Perspective), and between the differences within factor levels (i.e., Self Ego *minus* Self Allo vs Fam Ego *minus* Fam Allo: Identity*Perspective interaction).

Since this statistical approach is applied to the whole scalp, it raises the problem of multiple comparisons. To tackle this issue, we performed permutation tests (n permutations=1000) to assess the statistical significance of comparisons after multiple comparisons correction. Specifically, for each comparison between experimental conditions, a null distribution was generated by repeatedly shuffling the condition labels and recomputing the test statistics [64]. With this procedure, significant electrodes (with real t value greater than permutation distribution t values) were identified. A cluster was defined by the presence of at least three adjacent significant electrodes [65–70].

As control analysis [23], we performed the same statistics on the responses elicited at the base frequency (4 Hz and its harmonics, i.e., 8 Hz and 12 Hz) as dependent measure.

Statistical analyses were performed using MATLAB.

Behavioral analysis

In Experiment 3, to evaluate whether participants were able to explicitly detect the presence of their own hand under fast visual presentation conditions, we computed sensitivity (d') and response bias (criterion) using signal detection theory [26]. These measures were calculated separately for each perspective condition (Egocentric and Allocentric). In each block, the participant’s own hand was either included in the stimulation stream (Self conditions) or absent (Other conditions). Based on subjects’ responses (indicating whether their hand was present or not in the block), hits were defined as “yes” responses in blocks where the self-hand was present, while misses corresponded to “no” responses in those same blocks. False alarms were “yes” responses in blocks where the self-hand was absent, and correct rejections were “no” responses in those blocks.

Using the proportions of hits and false alarms, we computed d’ as an index of sensitivity to the presence of one’s own hand, and criterion as a measure of response bias. These values were then entered into two paired-samples t-tests, comparing d’ and criterion between Egocentric and Allocentric conditions to assess whether recognition sensitivity and decision strategy varied as a function of visual perspective.

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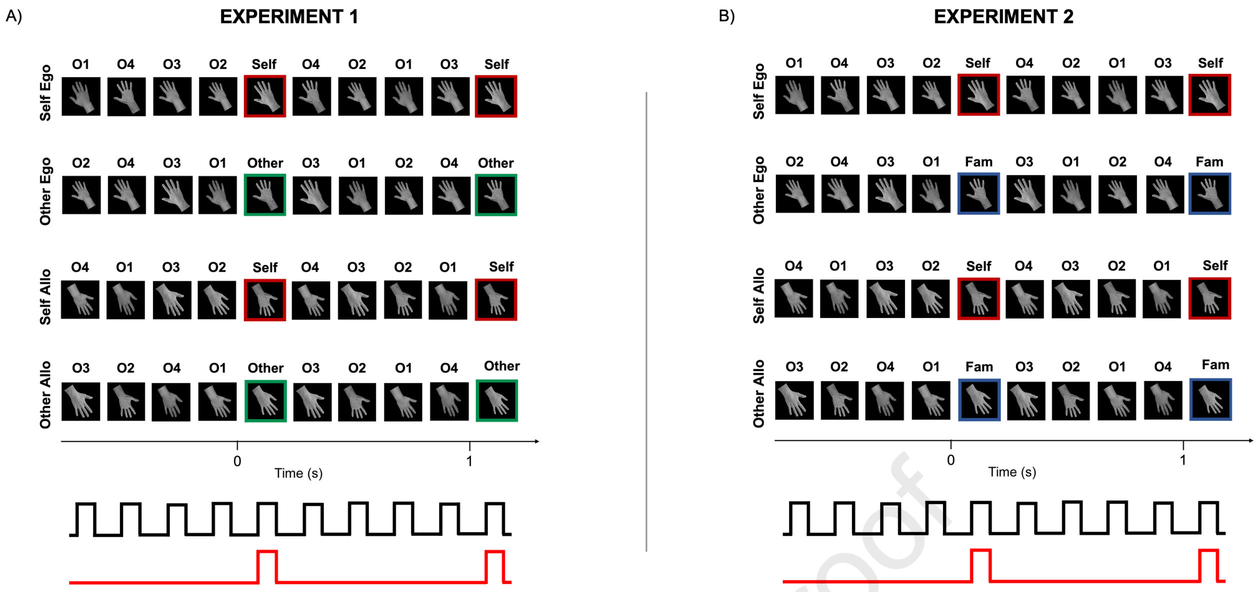
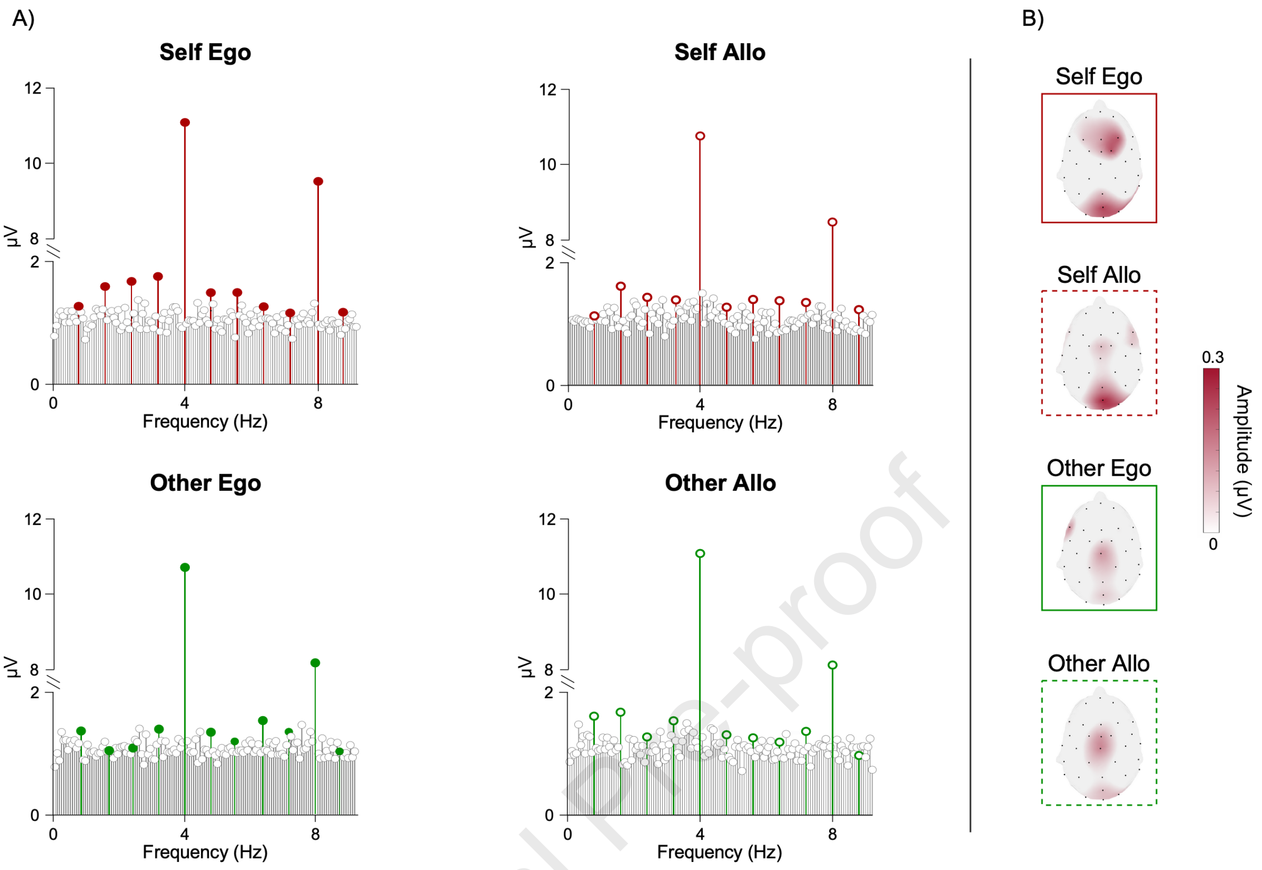
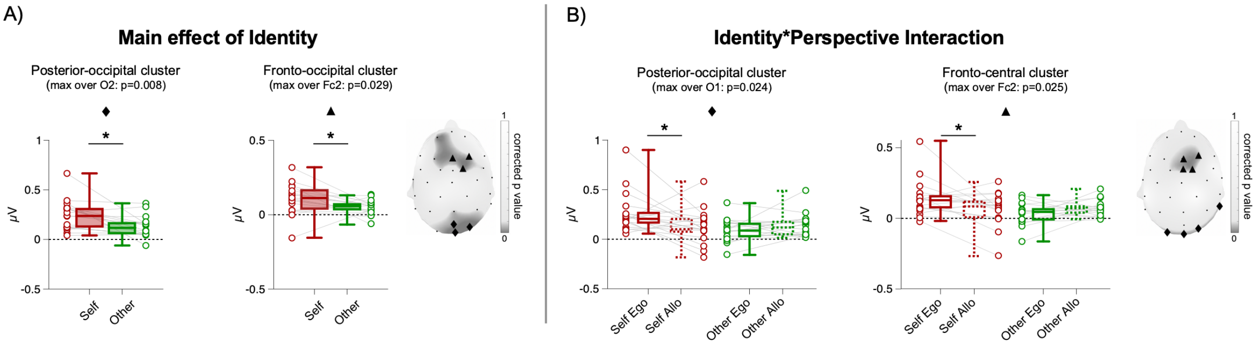
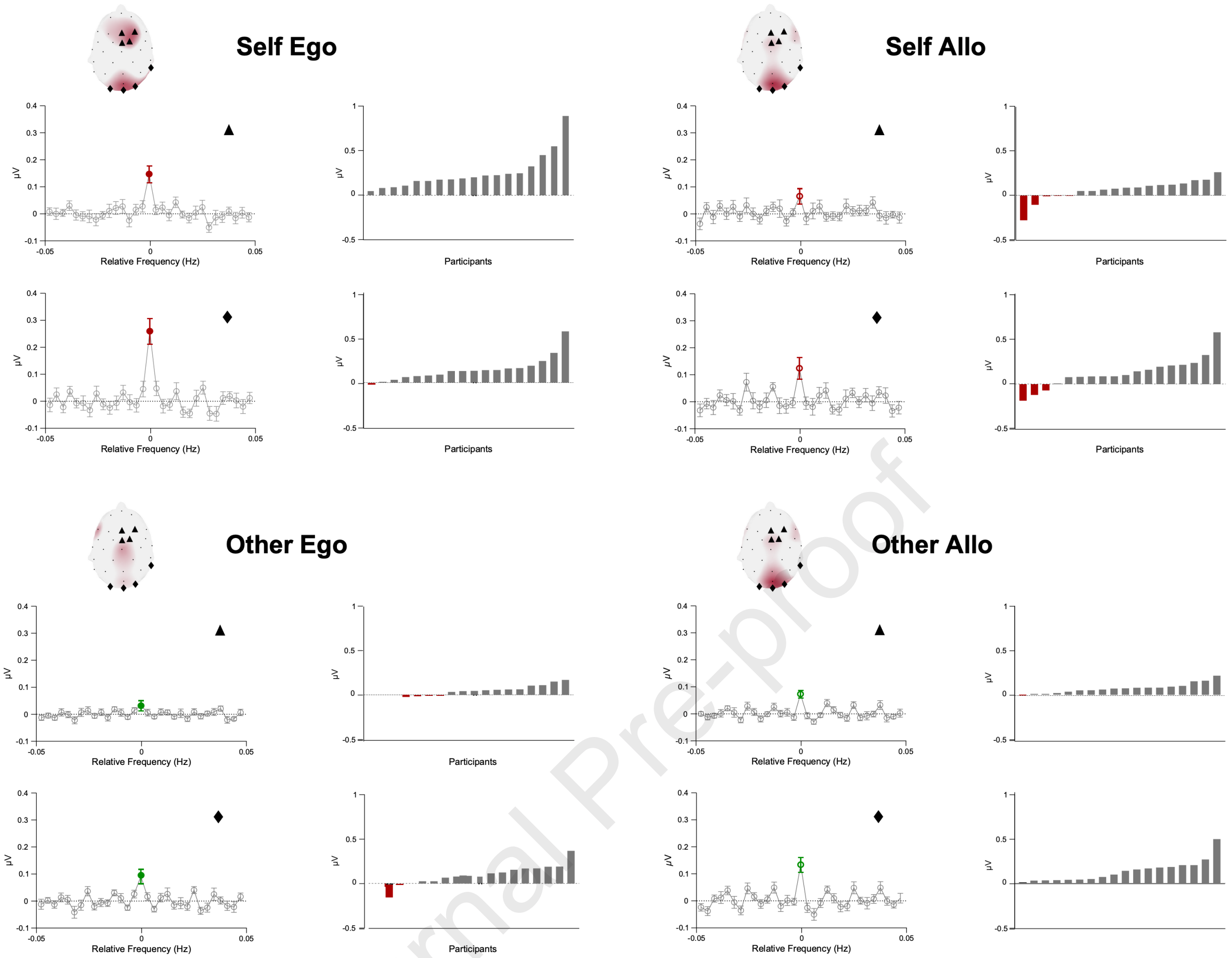
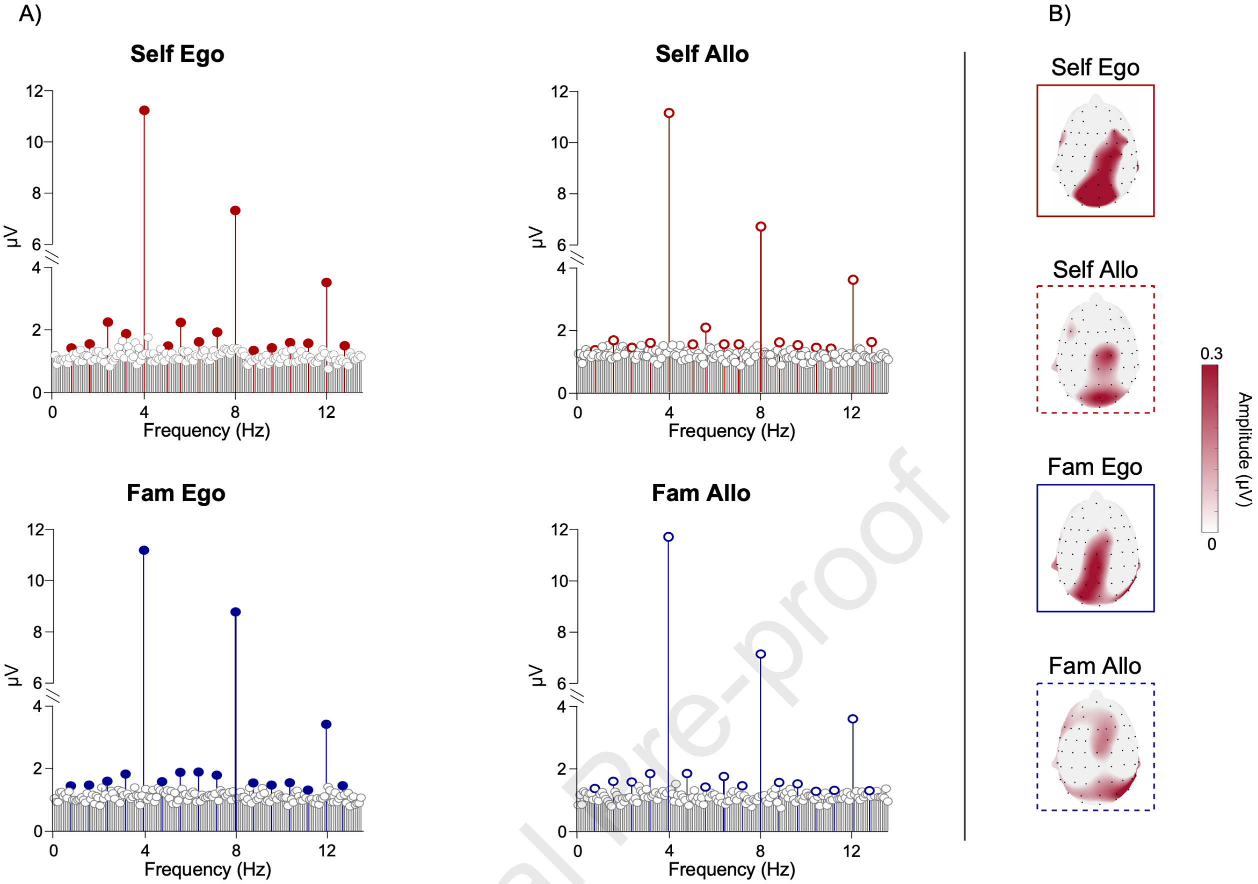
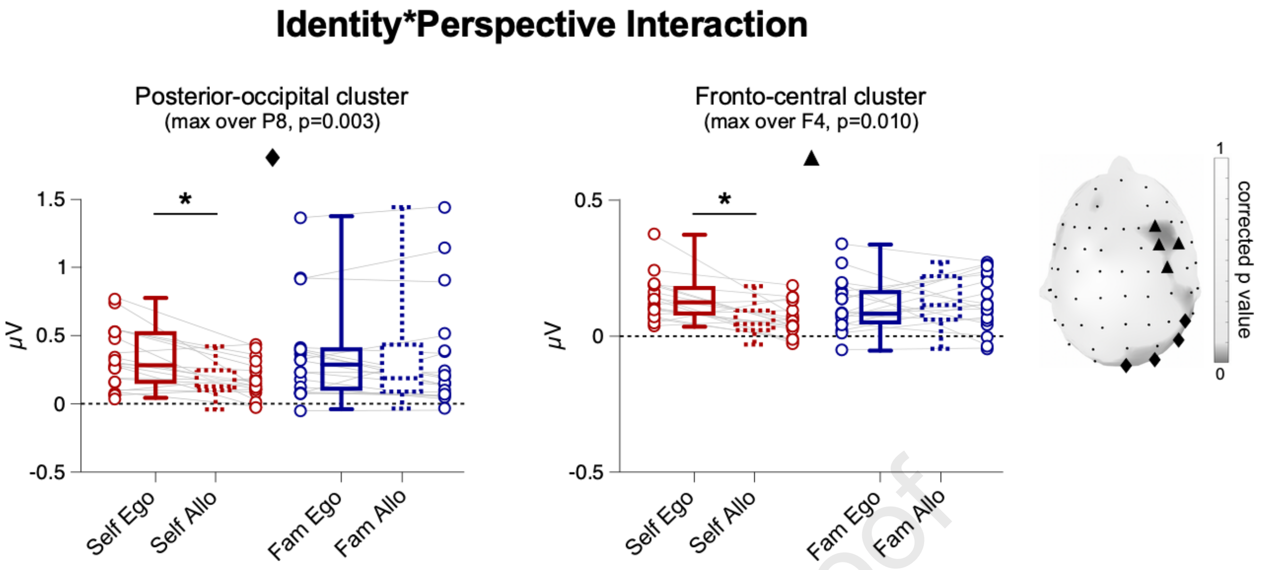

A)
EXPERIMENT 1
Self Ego
O1 O4 O3 O2 Self O4 O2 O1 O3 Self
Other Ego
O2 O4 O3 O1 Other O3 O1 O2 O4 Other
Self Allo
O4 O1 O3 O2 Self O4 O3 O2 O1 Self
Other Allo
O3 O2 O4 O1 Other O3 O2 O1 O4 Other
0
1
Time (s)
B)
EXPERIMENT 2
Self Ego
O1 O4 O3 O2 Self O4 O2 O1 O3 Self
Other Ego
O2 O4 O3 O1 Fam O3 O1 O2 O4 Fam
Self Allo
O4 O1 O3 O2 Self O4 O3 O2 O1 Self
Other Allo
O3 O2 O4 O1 Fam O3 O2 O1 O4 Fam
0
1
Time (s)

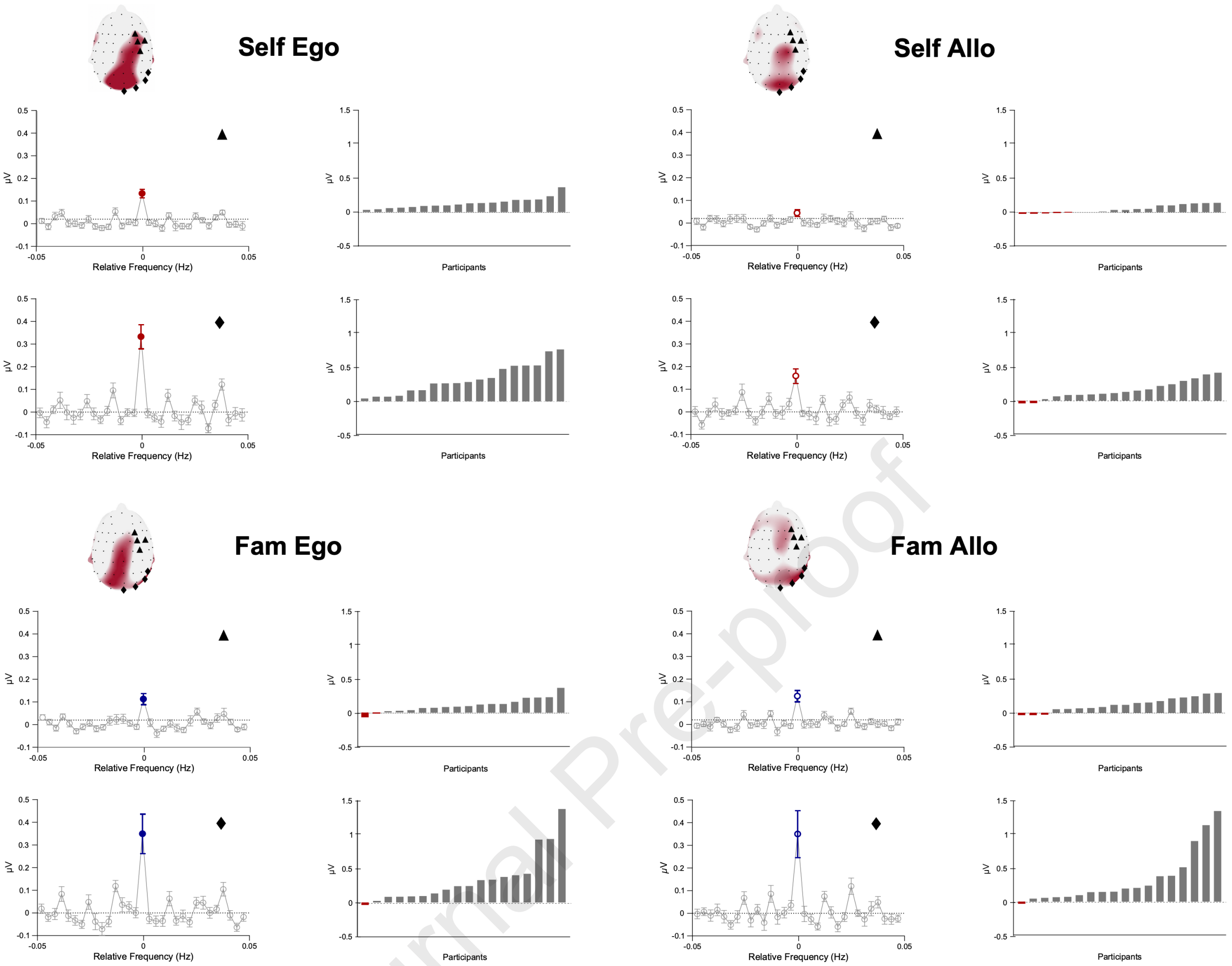

A)
Self Ego
Self Allo
Other Ego
Other Allo
12
10
8
2
0
μV
0
4
8
Frequency (Hz)
B)
Self Ego
Self Allo
Other Ego
Other Allo
0.3
0
Amplitude (μV)

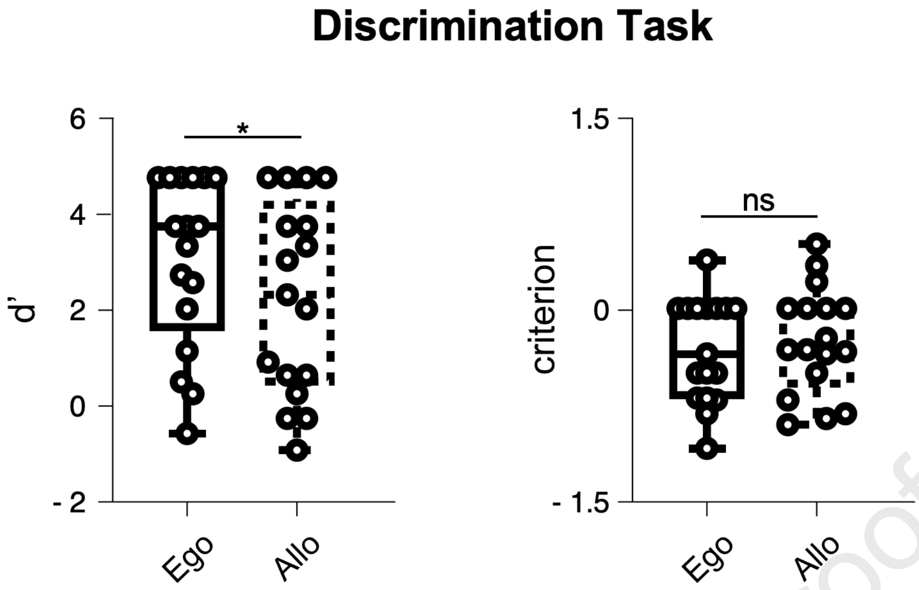

A)
Main effect of Identity
Posterior-occipital cluster
(max over O2: p=0.008)
Fronto-occipital cluster
(max over Fc2: p=0.029)
µV
1
0.5
0
-0.5
*
Self
Other
corrected p value
1
0
B)
Identity*Perspective Interaction
Posterior-occipital cluster
(max over O1: p=0.024)
Fronto-central cluster
(max over Fc2: p=0.025)
Self Ego
Self Allo
Other Ego
Other Allo


Self Ego
Self Allo
Other Ego
Other Allo
▲
♦
μV
0.4
0.3
0.2
0.1
0
-0.1
-0.05
0
0.05
Relative Frequency (Hz)
1
0.5
0
-0.5
Participants


A)
Self Ego
Self Allo
Fam Ego
Fam Allo
μV
0
2
4
6
8
10
12
0
4
8
12
Frequency (Hz)
B)
Self Ego
Self Allo
Fam Ego
Fam Allo
0.3
0
Amplitude (μV)


Identity*Perspective Interaction
Posterior-occipital cluster
(max over P8, p=0.003)
◆
1.5
1
0.5
0
-0.5
μV
*
Self Ego
Self Allo
Fam Ego
Fam Allo
Fronto-central cluster
(max over F4, p=0.010)
▲
0.5
0
-0.5
μV
*
Self Ego
Self Allo
Fam Ego
Fam Allo
1
0
corrected p value


Self Ego
Self Allo
Fam Ego
Fam Allo
▲
◆
μV
Relative Frequency (Hz)
-0.05
0
0.05
-0.1
0.1
0.2
0.3
0.4
0.5
Participants
-0.5
0.5
1
1.5



Discrimination Task

Highlights

- We investigated the neural mechanisms supporting hand identity discrimination

- We combined electroencephalography with fast periodic visual stimulation

- The self-hand image triggers stronger neural responses in egocentric perspective

- Self-hand recognition relies on visual–sensorimotor associations

Key resources table

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Datasets	This paper	https://data.mendeley.com/datasets/3rrbhbggxz/1
Software and algorithms		
E-prime 2.0	E-prime	RRID:SCR_009567
Matlab	MathWorks	RRID:SCR_001622
Letswave 6	NOCIONS	RRID:SCR_016414