Visual experience shapes bodily representation of emotion

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Abstract

Philosophers and experimentalists have long debated whether bodily representation of emotion is grounded in our sensory experience. Indeed, we are used to observe emotional reactions expressed through the bodies of others, yet it is still unknown whether this observation influences how we experience affective states in our own bodies. To delve into this question, we developed a naturalistic haptic task and asked a group of early (n=20) and late (n=20) blind, as well as sighted individuals (n=20) to indicate where in the body they perceive changes associated with affective states. Our results show that visual experience shapes bodily representation of emotion. Blind and sighted individuals attribute different importance to body regions in relation to specific emotional states, as sighted people focus more on visceral sensations, while blind report as more relevant the mouth and the hand areas. We also observe differences in the coherence of bodily maps of specific emotions, such as aggressiveness, for which early and late blind are homogenous in reporting the mouth, while sighted subjects demonstrate a scattered pattern of activation across the body. Finally, our findings show that blind people rely on a different organization of affect, as only sighted categorize bodily maps of emotion through the valence and arousal dimensions. In summary, we demonstrate that sensory experience impacts the bodily representation of affect by modulating the relevance that different body parts have in emotional reactions, by modifying the weights attributed to interoceptive and exteroceptive signals, and by changing how emotions are conceptualized in the body.

Keywords: emotion; embodiment; visual deprivation; feelings

Introduction

When we are all alone in the dark and we hear a sudden noise, we start feeling our heart pounding, cold shivers down our spine, we wide open our eyes and our muscles tense to prepare for a possible “fight or flight” response. This scenario highlights the fundamental role the body plays in the experience of emotions (Damasio, 1998; 2003), an idea central to pioneering work in affective sciences (e.g., Darwin, 1872; James, 1884).

Emotional states are commonly associated with facial configurations, body postures and gestures, visible physiological responses, such as the increase in sweating or change in skin colors; as well as invisible ones, such as the change in heartbeat and blood pressure (Levenson, 2003; De Gelder et al., 2015). This variety of nonverbal visual cues provides crucial information to others about the pleasantness and intensity of one's current experience (Ekman and Cordaro, 2011; Tracy et al., 2015), while interoceptive information primarily influences the subjective one (Wiens, 2005; Critchley and Garfinkel, 2017). Interestingly, all these signals are integrated into a conceptual representation of somatic reactions specific to emotions, which can be accessed by asking individuals where in the body they perceive changes during affective states (Nummenmaa et al., 2014). Indeed, bodily maps represent a powerful tool to explore differences and similarities in the bodily representation of emotions across disorders or conditions (e.g., Torregrossa et al., 2019; Lyons et al., 2021; Niemi et al., 2024). In these studies, researchers typically employ an exploratory approach in which the bodily maps of the two groups are compared in a pixelwise manner, so as bodily parts covarying with individuals’ characteristics, emerge without any specific a priori hypothesis. The embodiment theory suggests that we use our bodies to simulate what other people are experiencing and better understand their emotions (e.g., Niedenthal et al., 2005). Bodily

reactions, therefore, assume both an external communicative function and an internal regulatory one (Damasio, 1998; 2003; Tsuchiya and Adolphs, 2007).

The relevance of the senses in capturing the affective communicatory cues coming from other individuals seems evident (e.g., Itier and Batty, 2009). However, while the importance of this perceptual experience is clear, its precise role in shaping the bodily representation of affect remains poorly understood. In addition to sensory input, language serves as a pivotal medium through which individuals communicate and interpret their emotions (Lindquist et al., 2016). Through language, individuals label and articulate their emotions, attributing meaning to internal states and external stimuli. Furthermore, cultural and social norms embedded within language influence how emotions are expressed and perceived within different contexts (Jackson et al., 2019). Concepts and metaphors associated with emotions can vary across cultures, potentially influencing where individuals locate their emotional experiences in the body (e.g., butterfly in the stomach).

Yet, there remains uncertainty regarding to what extent individuals rely on sensory input to comprehend and communicate their own emotional bodily experiences. In other terms, it is unknown whether witnessing emotional reactions in others is instrumental, or in contrast epiphenomenal, when it comes to shaping our own emotional range and bodily responses. Both historical (James, 1884) and modern (Damasio 1998, 2003) theoretical models on emotional representation in the body operate under the assumption that our affective experiences are initiated by perceiving emotion-related bodily states, reflecting alterations in the skeletomuscular and autonomic nervous systems, among others. This assumption raises the fundamental question of whether innate mechanisms alone suffice for the bodily experience of affect, or if sensory development and personal experiences also play crucial roles in the representation of emotions in the body. For instance, becoming red in our

cheeks is the most common reaction associated with embarrassment. If an individual has never been able to observe this effect in others, would they still hold a bodily representation of embarrassment that involves the cheeks? If the somatic component is dominant compared to the communicative one, it would be possible, while if the opposite is true, we would find a different representation of emotions.

Vision is the sense humans rely the most to gather information from the external world (Kandel et al., 2000; Pike et al., 2012). Being sight also fundamental for processing affective visual cues, the question of whether blindness impacts the perception and experience of bodily reactions is particularly compelling. Recent evidence has shown how blind people develop different tactile and auditory affective abilities (Martins et al., 2019; Falagiarda et al., 2023; Radziun et al., 2023a), as well as enhanced cardiac interoception (Radziun et al., 2023b). Of note, blind individuals report difficulties in social interactions in relation to inaccessible visual signals, especially in understanding positive exchanges (Qiu et al., 2015). On the other hand, previous studies have highlighted similar performances between early blind and sighted individuals in different social cognition domains, such as Theory of Mind (Bedny et al., 2009), and a similar brain representation of emotional instances (Lettieri et al., 2024). Specifically concerning the bodily expression of emotional states, facial expressions emerge as fundamental components of nonverbal communication, visibly reflecting underlying emotional states and facilitating affective information exchange between individuals (e.g., Matsumoto et al., 2008). However, ongoing debates persist regarding the origin of emotional facial expressions, questioning whether they are innate or develop through exposure to visual cues during early development. On the one hand, the observation of similar spontaneous expressions between blind and sighted individuals (Galati et al., 1997; 2003), suggests the presence of innate mechanisms for emotional expression. On

the other hand, difficulties arise when blind individuals attempt to consciously control their facial expressions or interpret the facial expressions of others, indicating a potential reliance on visual learning to develop these skills (for a review see Valente et al., 2018). This paradox raises intriguing questions about the interplay between innate biological factors and environmental influences in shaping emotional expression and recognition. Furthermore, it underscores the need for further research to elucidate the mechanisms underlying emotional processing in the absence of vision and potential strategies for enhancing emotional communication and understanding among blind individuals.

Considering all this, whether and how the lack of vision impacts the conceptual representation of bodily emotions remains unknown. Moreover, the duration of time spent without visual inputs may significantly influence how individuals perceive and represent emotions in the body.

In conducting this study, we adopted an exploratory research strategy primarily to generate hypotheses for future investigations. This approach provides the flexibility needed to understand complex phenomena and uncover underlying mechanisms, particularly when existing theories are limited. In such cases, exploratory studies can offer valuable insights and ideas for developing future hypotheses, although they may not provide definitive evidence for or against existing claims (Ledgerwood, 2019). By employing this strategy, we aimed to open new avenues for future research and lay a foundation for subsequent studies.

The goal of the present research was, therefore, to explore whether visual experience plays a role in shaping our bodily emotion repertoire, addressing a longstanding question about how the embodiment of emotions happens. To do so, we adapted a previously validated visual paradigm (Nummenmaa et al., 2014) to the haptic modality (Lettieri et al., 2023), and

asked a group of early blind, late blind and sighted individuals to indicate where in the body they perceive changes associated with positive and negative affective states.

Materials and Methods

Participants. A group of sighted (n = 20, 10F, mean age 43.3±15.7 years; high school diploma 20%, Bachelor's degree 45%, Master's degree or higher 35%), early (n = 20, 8F, mean age 42.7±11.2 years; high school diploma 50%, Bachelor's degree 40%, Master's degree or higher 10%), and late blind individuals (n =20, 10F, mean age 45.5±11.4 years; high school diploma 60%, Bachelor's degree 25%, Master's degree or higher 15%) took part in the study. Of note, we conducted a power analysis to determine our sample size, as detailed in Supplementary Materials. No significant difference in the years of age ($F = 0.32$; $p = 0.729$) nor education level ($\chi^2 = 8.68$; $p = 0.070$) was found when comparing the three groups. All participants were French native speakers, and we report in Table 1 the details of the causes of sensory deprivation and residual perception for our volunteers. The requirement for participation for sight-deprived subjects was complete blindness or having only minimal light sensitivity without the ability to functionally use this feeling at the time of testing. Before the beginning of the experiment, the procedure and risks associated with their participation were clearly explained, and volunteers signed an informed consent, having the right to withdraw at any time. Importantly, all study participants demonstrated full functionality and autonomy. Documents were read to sight-deprived participants by a native French speaker, and the placement of their signatures was guided. Subjects answered either verbally or in writing to the Positive and Negative Affective Schedule (PANAS; Watson et al., 1988), the State-Trait Anxiety Inventory (STAI-Y2; Spielberger, 1983), and the Toronto Alexithymia Scale (TAS; Bagby et al., 1994) to assess their mood, trait anxiety, and alexithymia levels, respectively. Sighted subjects were on average more anxious ($p < 0.05$; mean 43.8±8.5) than early (mean 34.7±10) and late blind individuals (mean 39.9±10), but at

the time of testing, we found no differences in negative mood ($p > 0.05$; early 12.7±3.7; late 13.9±4.6; sighted 12.8±2.8). Also, alexithymia levels were comparable across groups ($p > 0.05$; early 41.4±11.3; late 45.8±12.4; sighted 47.3±9.7). The study was conducted in accordance with the Declaration of Helsinki and was approved by the local IRB (CEHF: Comité d'éthique hospitalo-facultaire; Protocol No. B403201628743). Participants received monetary compensation for their participation.

—- insert Table 1 —--

Table 1. Demographic and sensory deprivation characteristics of early and late blind participants. High-school diploma refers to either 11 or 12 years of education, depending on the national education system. Bachelor's degree includes individuals with professional diplomas, having at least 13 years of education.

Experimental setup. A 3D mannequin representing a genderless human body was mounted on a wood structure and on its floor was installed a tripod holding a camera on top, to which was attached a ring light to control luminance (Figure 1A in Lettieri et al., 2023). The structure was fixed in its position on a table. For a 3D exploration of the experimental room and apparatus used in the study, please visit the following links: https://shorturl.at/oxH68; https://shorturl.at/wKQV2.

Thirty emotional terms were employed in the study, balanced between positive and neutral (n=16) and negative (n=14) states, according to valence score (from 1 to 7) reported in Gilet et al., 2012: tenderness (valence = 6.0), love (valence = 5.9), alert (valence = 5.9), calmness (valence = 5.7), attraction (valence = 5.6), joy (valence = 5.6), enthusiasm (valence = 5.5), ecstasy (valence = 5.4), pleasure (valence = 5.3), euphoria (valence = 4.8), amazement (valence = 4.6), exaltation (valence = 4.6), excitement (valence = 4.4), curiosity (valence = 4.3), astonishment (valence = 4.1), nostalgia (valence = 4.0), embarrassment (valence = 3.6), agitation (valence = 3.4), nervousness (valence = 2.9), repulsion (valence = 2.3), anxiety

(valence = 2.2), sadness (valence = 2.2), fury (valence = 2.2), panic (valence = 2.2), terror (valence = 2.1), disgust (valence = 2.1), wrath (valence = 2.0), horror (valence = 1.6), aggressiveness (valence = 1.5) and despair (valence = 1.5). Recordings of subjects' responses were carried out by a high-resolution camera (1080p, 60fps).

Experimental procedure. All participants had no previous visual information of the experimental setup and sighted controls were blindfolded with a professional eyeshade (Goalfix Eclipse) for the entire duration of testing and before entering the experiment room. Subjects sat comfortably in front of a table with the mannequin on top, and they could easily and freely interact with it. Before the beginning of the task, subjects had to indicate eight organs and body parts on the mannequin (e.g., heart, liver, elbows, calves) to ensure they had reached a good level of understanding of and interacted sufficiently with the body figure. A round green sticker was applied on the nail of the index of their dominant hand (Figure 1B in Lettieri et al., 2023). During the experiment, participants were free to explore the mannequin with both hands, but they had to provide their answers only with that finger. For the task, subjects had to indicate which parts of the body they typically felt becoming activated when feeling each emotion presented to them. For each trial, the instructions were: "*Think about when you feel emotion, mark with your finger as if it were to color all the areas of the body where you perceive an increase in their activity*." Participants were instructed to think about their personal experiences and freely report what they usually perceived in their body. In each trial, the camera was activated by one of the experimenters using a remote as soon as the participant's hands left the wooden platform and were filmed for the time the participant explored the mannequin. The camera was stopped after the hands of the volunteer touched the wooden platform again so that for each participant and emotion, a brief video was obtained. The order of trials was randomized between participants.

Transparency and Openness. We report how we determined our sample size, all data exclusions and manipulations, missing data, and all relevant measures in the study following the Journal Article Reporting Standards (JARS; Kazak, 2018). Data, analysis code, and research materials are publicly available and can be accessed at: https://osf.io/e8gr6/?view_only=86bdca872aca4f2588f31f8ed07de333 or by emailing the corresponding authors (giada.lettieri@uclouvain.be; olivier.collignon@uclouvain.be). This study's design, hypotheses, and analyses were not preregistered.

Preprocessing of bodily maps. As the camera employed for tracking the participants' hand movements was detachable, the initial phase of generating group-level emotional bodily maps involved aligning the videos from each trial and participant to a shared body silhouette. This process helped to compensate for possible misalignments between experimental sessions. For this purpose, we initially marked 24 red dots on the mannequin and recorded a short video of it. The first frame of this template video was imported into MATLAB and used as a reference (i.e., fixed image) in a semi-automated alignment procedure. To carry out the alignment, the initial frame of each experimental session's first video (i.e., moving image) was also imported into MATLAB, and the cpselect function was employed to manually identify the coordinates of the 24 markers on both the fixed and moving images, corresponding to the red dots. Subsequently, a projective geometric transformation was fitted to the pairs of control point coordinates using the fitgeotrans function. Lastly, each video frame of the trial was aligned to the template frame by applying the computed geometric transformation with the imwarp function (linear interpolation) and using the grid and dimension of the template video as a reference frame. The subsequent step to obtain group-level bodily maps involved segmenting the green marker on the index finger's nail of the participant's dominant hand and reconstructing its trajectory during the haptic exploration of

the mannequin. To this aim, we imported the video of each trial into MATLAB once it had been aligned to the common template. Then, each video frame was converted from the RGB to the CIE 1976 L*a*b* color space using the rgb2lab function. An optimal color threshold was manually defined in the L*a*b* space by visually inspecting the segmented version of the marker and interactively adjusting the values. The thresholding procedure generated a binary mask for each frame, in which pixels with value 1 (i.e., "true") denoted the marker on the participant's fingertip, while those with value 0 (i.e., "false") represented the remaining part of the image. To reconstruct the trajectory of the segmented marker over time, we first used the bwpropfilt function to retain only the largest connected region surviving the color threshold. Then, we addressed potential holes in the segmented region with the imfill function and estimated the centroid coordinates of the resulting cluster of pixels using the regionprops function. In line with previous emBODY implementations (Nummenmaa et al., 2014), the trajectory of the marker was masked with a silhouette of the mannequin, which was drawn by one of the experimenters using the drawpolygon routine and the template frame as reference. For further details on the preprocessing pipeline and validation of the method, please see Lettieri et al., 2023.

To account for between-participant variability in the drawing, we applied a 2D Gaussian filter with $\sigma = 10$ pixels to the coordinates obtained from the segmentation step to the single-participant bodily maps. We set the maximum amplitude of the filter to 1 so that the exact coordinates of the centroid at each frame were assigned with this value, whereas neighboring pixels had lower probability values depending on the filter σ. Because neighboring Gaussian filters were combined into a single bodily map, the maximum value observed across pixels depends on the time spent by the participant on a specific body area. To uniform data coming from different volunteers, we thus divided the pixel values by the maximum of the bodily

map within each participant. The single-participant smoothed bodily maps of emotion were visually inspected, and the procedure quality was evaluated by comparing the marker trajectories with the original videos. Also, group-level bodily maps of emotion were obtained by computing for each pixel the between-participant average. As a standard preprocessing procedure for subsequent analysis, individual participant maps underwent downsampling to reduce the resolution to 20% of the original size, effectively decreasing the number of pixels. Additionally, any pixels outside the body silhouette, which served as the focal area in the study, were eliminated from consideration, resulting in the creation of a masked image (Nummenmaa et al., 2014).

Pixelwise test of the effect of sensory deprivation across emotions. Based on the above procedure, we obtained the bodily maps for each emotion and subject, then averaged across affective states. First, for each pixel in the masked image, we computed the difference between early blind, late blind, and sighted individuals using a non-parametric one-way analysis of variance (i.e., Kruskal-Wallis test), obtaining both the chi-square and the mean ranks of comparisons between all group pairings. By shuffling group membership (n = 1000 permutations), we computed the pixelwise uncorrected p-values of the chi-square of group differences. We then applied a cluster forming threshold of $p < 0.001$ to the permuted and unpermuted maps of group differences to determine clusters of pixels. For the unpermuted versions, we retained the size of all clusters. Instead, the family-wise corrected null distribution was obtained by measuring the size of the largest cluster in each permuted bodily map. After, we computed the family-wise corrected p-value of each unpermuted cluster of differences between groups in bodily maps of emotions. To rule out the possibility that differences between groups are merely driven by how the task is performed, we conducted a control analysis evaluating whether overall traveling distance across emotions was associated

with sensory experience. To this aim, for each participant and emotion, we computed the euclidean distance between the x,y coordinates of the marker obtained from consecutive video frames. This resulted in a set of euclidean distances, one for each pairing of consecutive timepoints, that summed together measured the overall traveling distance of the finger of the participant for each emotion. To summarize the participants' characteristics in the exploration of the mannequin we estimated the average traveling distance across emotions. By repeating this procedure for all participants we obtained 60 mean overall traveling distances which we used as the dependent variable in a non parametric anova (Kruskal Wallis) assessing differences between sighted and early and late blind individuals. As a further step to ensure that there were no differences in how participants explored the mannequin, we also directly compared all possible group pairings on traveling distance using Wilcoxon rank sum test.

Association between time spent as blind and bodily maps. We investigated the association between time spent as blind, i.e., the age at testing minus the age at blindness onset, and the extent to which early and late blind participants indicated a specific body part across all tested emotions. This relationship was assessed in a region of interest (ROI) obtained from the pixelwise test described in the previous paragraph. In more detail, we identified a specific area within our images that we focused on for analyzing further. For each blind individual, we computed the within-ROI mean pixel intensity of bodily maps averaged across different emotions. This process allowed us to investigate and compare the intensity of bodily sensations represented in the specified region among different emotional states. The resulting values (one per participant) were included as dependent variable in a general linear model, having time spent as blind as the only predictor. The significance of the relationship was established at $p < 0.05$. As a control analysis, all other things being equal, we added to

the general linear model the age at testing as a second predictor, such that its potential confounding effect was attenuated.

Emotion-wise assessment of sensory deprivation. We then considered all bodily maps of all our subjects for each emotion and created a 2D matrix in which each row represented a participant and each column the pixels of their maps. Using Pearson's coefficient, we computed pairwise correlations of bodily maps between all possible subject pairings, thus obtaining a Representational Dissimilarity Matrix (bodily maps RDM), a mathematical construct used to quantify the similarity or dissimilarity between different neural or cognitive representations. Here, each bodily map represents the bodily sensations associated with different emotions for each subject. By computing correlations between these bodily maps for all pairs of subjects, we obtained the RDM matrix where each cell represents the dissimilarity or similarity between the bodily maps of two individuals. Furthermore, starting from a vector indicating the identity of our sample (early blind, late blind and sighted controls), we computed Jaccard's distance to generate a group membership RDM. We then tested the association between our group membership RDM and the bodily maps RDM using Kendall's tau correlation coefficient. By doing this, we tested whether the within-group pairwise association of bodily maps was higher than the one between groups. Statistical significance of this association was obtained through a permutation test (n = 2,000) in which the group membership RDM was maintained fixed while at each iteration the identity of subjects was shuffled and a new bodily maps RDM was generated. The null distribution resulted from the computation of Kendall's tau coefficient between the group membership RDM and each permuted version of the bodily maps RDM. This procedure was repeated for each pair of groups in our sample (early and late blind, early and sighted, late and sighted). Results were corrected for the number of group comparisons using Bonferroni within each emotion.

Measuring the effect of sensory experience on the arrangement of emotions in the space of bodily maps. Starting again from each bodily map of emotions of our groups, we collated the average of them across subjects pertaining to the same group. By doing this, we obtained 30 bodily maps for early and late blind and sighted controls. Then, for each group, we created a matrix in which each row is an emotion and each column the pixels of our map. The association between emotions in each group is assessed with Pearson's coefficient, resulting in an array of correlation values (30*29/2) for each matrix (RDM). We then tested the relationship between all pairs of RDM with Kendall's tau correlation coefficient and on the three values obtained we assessed the statistical significance. To do so, we shuffled 1,000 times the group identity while ensuring that no emotion was repeated in each group. At each iteration, we computed the association between null RDM pairs with Kendall's tau coefficient and the position of its value in respect of the null distribution provided us the p-value for each pair of RDM. In addition, we tested for each group whether the similarity in bodily maps was associated with the position of the emotional state in the valence and arousal dimensional space. Specifically, we extracted our 30 affective states from the French Emotional Evaluation List, a database of 835 terms rated according to their valence and arousal levels (Gilet et al., 2012). In the case of five terms that were not reported in the database, we considered either their noun version instead of the adjective ones, or we chose the respective term from the English translation. We then generated a dissimilarity matrix between emotions starting from the valence and arousal scores and calculating the Euclidean distance in a pairwise manner between all possible pairs of affective states. By following this procedure, we obtained an array of 30*29/2 values that were then correlated through Kendall's tau with the RDM obtained from the bodily maps of each group. Statistical significance was obtained by shuffling 2,000 times the rows of the affective norms matrix and by recalculating the

association between RDM groups under the null hypothesis. Results were corrected for the number of group comparisons using Bonferroni. We complemented this analysis by correlating each group RDM with the dissimilarity between emotions calculated by specifically relying either on valence or on arousal scores. As detailed above, statistical significance was assessed through non parametric permutation testing. We did this to investigate whether the potential association between bodily maps RDM and affective norms was specific to valence or arousal and whether this specific association was found in all groups.

Low dimensional embedding of bodily maps of emotions. For each experimental group, we averaged the bodily maps per emotion, obtaining 30x60 images. Then, we applied Nonnegative matrix factorization (NNMF) using the alternating non-negative-constrained least squares method (Kim and Park, 2007). The number of factors was established following the method proposed by Brunet and colleagues (Brunet et al., 2004). We normalized factor weights between 0 and 1, and we graphically represented the spatial distribution of factors in our body silhouette. We also report the top five emotions having the highest weight on each factor. The analysis was conducted using the MATLAB toolbox developed by Li and Ngom (2013).

Results

Pixelwise test of the effect of sensory deprivation across emotions. To assess the effect of sensory deprivation on the representation of emotions in the body, we first investigated differences across early blind, late blind and sighted individuals in their group-averaged bodily maps. Specifically, we explored in a pixelwise manner whether specific areas of the body were more involved in the representation of emotions across groups. We find that the stomach region is differently indicated by sighted compared to congenitally deprived individuals ($p_{FWC} < 0.05$; Figure 1). Of note, we observe a similar finding in the comparison between sighted and late blind subjects, even if it does not survive the correction for multiple comparisons. Moreover, we found no group differences in how participants performed the exploration of the mannequin as measured by the traveling distance ($\chi^2_{(2)}=1.613$, p-value = 0.446; sighted controls vs early blind: z-score = 1.150, p-value = 0.250; sighted controls vs late blind: z-score = 0.203, p-value = 0.839; early blind vs late blind: z-score = -0.987, p-value = 0.324).

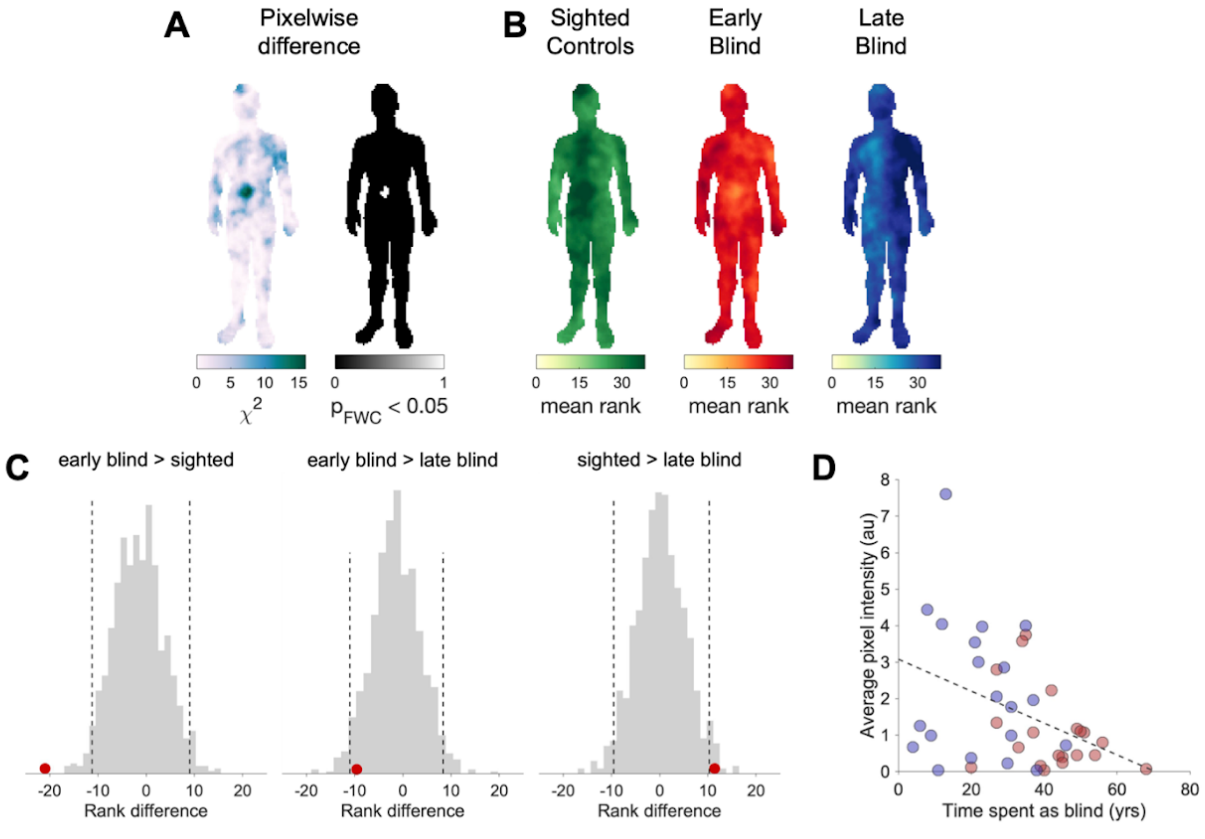
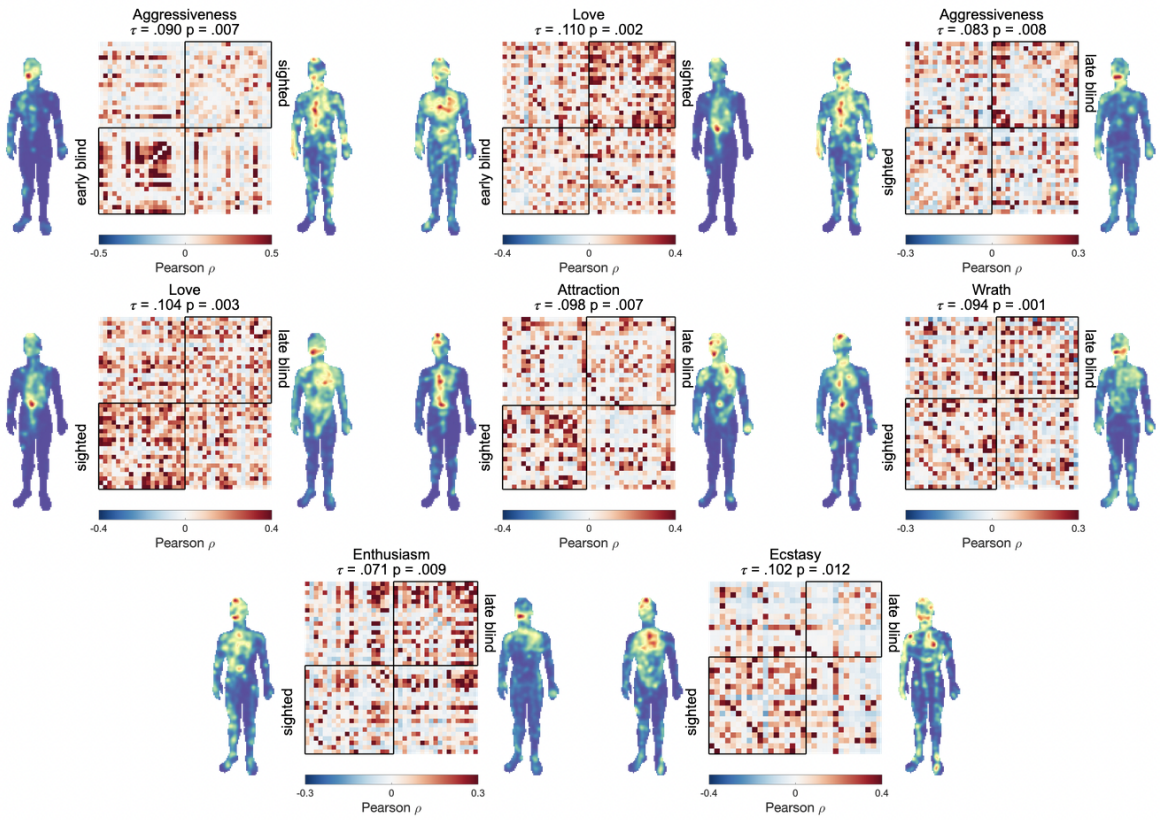


Figure 1. Pixelwise difference across emotions. In Panel **A**, we report the χ^2 of the pixelwise test across emotions on the left side of the image, and, on the right, the statistically significant cluster of the omnibus test. Panel **B** depicts from left to right the mean ranks of sighted, early and late blind individuals, respectively. In panel **C**, we report the null distribution for the difference between all group pairings averaged across pixels of the significant cluster. Red dots represent the group difference averaged across pixels for the three contrasts. Panel **D** depicts the scatter plot showing the association between time spent as blind (in years) and the extent to which blind individuals indicated the stomach region across all emotions. Red dots represent early blind subjects, while blue points late ones.

Association between time spent as blind and bodily maps. We then explored whether the duration of blindness influences the localization and intensity of bodily sensations associated with emotional states. Specifically, with a general linear model, we tested the association between time spent as blind (i.e., age at testing minus age at blind onset) and the extent to which early and late blind participants indicated the stomach area across all tested emotions (i.e., the region of the body showing significant group differences). Results show that the time spent as blind relates negatively to the involvement of the stomach area in bodily maps of emotions (Figure 1D; $\beta = -0.044$; 95CI = [-0.077, -0.011]; $t = -2.680$; p-value = 0.0108), that is the longer people are sight deprived the less they report bodily sensations in the stomach region. This finding is corroborated even when age at testing is added to the model as a covariate ($\beta = -0.039$; 95CI = [-0.074, -0.004]; $t = -2.282$; p-value = 0.0283). Of note, we found no significant associations between age and pixel intensity in the stomach region both in blind participants ($\beta = -0.037$; p-value = 0.116) and in sighted people ($\beta = -0.020$; p-value = 0.765).

Emotion-wise assessment of sensory deprivation. Then, we explored possible differences and similarities in the bodily representation of affective states for all our experimental groups. To answer this question, for each emotion, we tested whether the within-group pairwise correlation of bodily maps was higher than the one between groups. The similarity in bodily



maps of aggressiveness, love, attraction, wrath, enthusiasm, and ecstasy depends on sensory experience ($p_{Bonf} < 0.05$; Figure 2). Specifically, early blind show a higher similarity for the state of aggressiveness, as they consistently report the mouth region compared to sighted participants, in which there is a spread involvement of almost all body parts. A similar pattern is observed for late blind, who provide more coherent bodily maps compared to sighted, reporting a strong involvement of the mouth and the hands. In the case of love, instead, sighted participants are characterized by a higher inter-subjects consistency in bodily maps, with a focus on the stomach area, differently from both early and late blind individuals who indicate more the chest and face regions. Moreover, in the comparison between sighted and late blind, we observe that sighted show a statistically significant higher agreement in the bodily map of ecstasy and attraction, in which they focus on the head, heart and stomach areas. In the case of wrath and enthusiasm, instead, late blind consistently report the mouth region.

Figure 2. Emotion-wise assessment of group differences. Representational Dissimilarity Matrices (RDMs) for statistically significant emotions in which the within-group pairwise association of bodily maps was higher than the one between groups. Each RDM represents a significant emotion, and red indicates a stronger between-participant correlation. The average bodily map of each group for that emotion is reported next to the corresponding label, and hot colors represent the overlap between reports of individual participants.

Measuring the effect of sensory experience on the arrangement of emotions in the space of bodily maps. Also, we investigated whether the bodily maps of emotions were organized in a similar manner across sensory deprived and sighted individuals. To do so, the projection of emotions in the space of bodily maps as a function of sensory experience was explored using Representational Dissimilarity Matrices expressing the closeness of group-averaged maps for each emotion and each group. Our findings show that there is a significant correlation in how early and late blind subjects report bodily maps of emotion ($p_{Bonf} < 0.05$; Figure 3B,C). Instead, sighted people show a distinctive pattern of the relationship between emotions in the space of bodily maps (Figure 3A). Furthermore, we tested the underlying organization of emotions in our samples, and investigated whether the dimensional model of valence and arousal was at the base of the representation of emotions. Results show that sighted participants organize bodily maps of emotion following the valence and arousal dimensions ($\tau = -0.103$, p-value = 0.032; Figure 3D), while the same is not true for early ($\tau = -0.013$, p-value = 0.705) and late ($\tau = 0.036$, p-value = 0.374) blind subjects. Moreover, when we considered valence and arousal separately, we found that the similarity in bodily maps of sighted was specifically related to the similarity of emotions in terms of arousal ($\tau = -0.144$, p-value = 0.029), but not valence ($\tau = -0.057$, p-value = 0.114). In line with the previous results, for the sensory deprived groups, we found no significant association with valence or with arousal (early blind valence: $\tau = -0.019$, p-value = 0.528; early blind arousal: $\tau = 0.012$,

p-value = 0.906; late blind valence: τ = 0.034, p-value = 0.323; late blind arousal: τ = 0.058, p-value = 0.284).

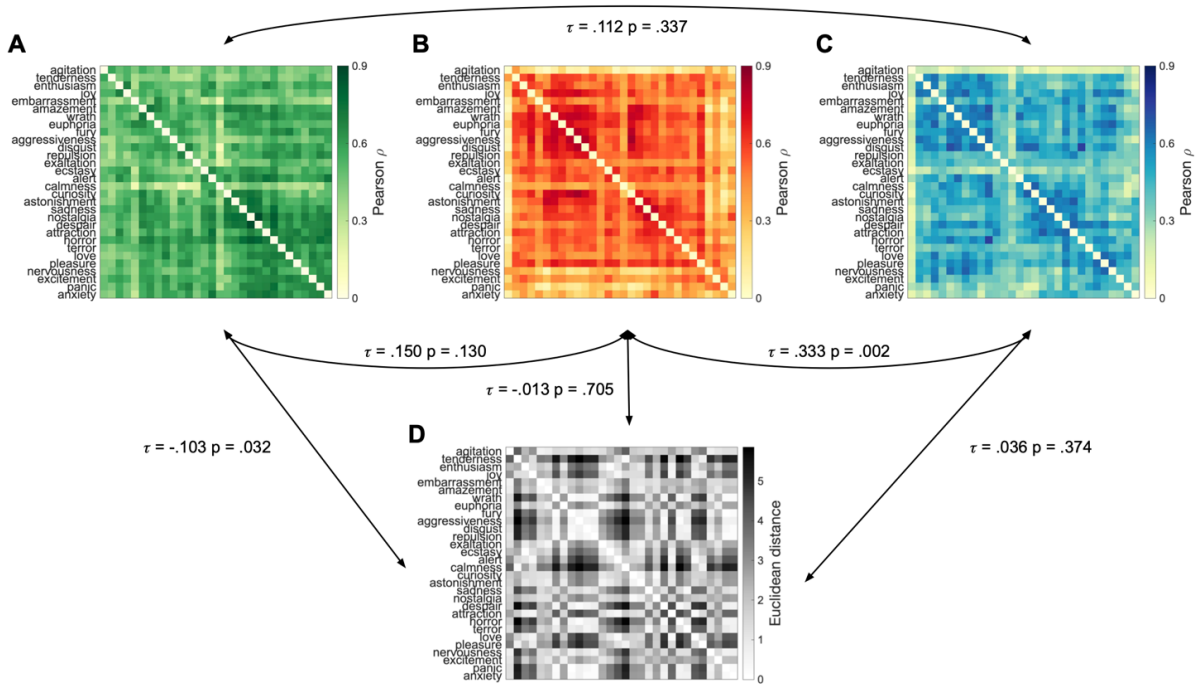


Figure 3. Between-group association of the similarity in bodily maps of emotions. Panels (**A-C**) report the emotion-by-emotion RDMs for the group of sighted (**A**), early (**B**) and late (**C**) blind. In panel (**D**) the valence and arousal dimensional space RDM is reported.

Low dimensional embedding of bodily maps of emotions. Lastly, using the nonnegative matrix factorization method, we tested the existence of specific components in our bodily maps. We find two most reliable factors, where the first one is the head region, while the second is the rest of the body (Figure 4). Interestingly, for the first factor, we observe that the region with the highest loading in sighted is the top of the head, while early and late blind focus more on the eyes and mouth areas. The second factor, instead, is maximally expressed in the stomach region for sighted individuals and in the upper torso and the hand area in blind participants. The second factor also includes the mouth region in the late blind group only. The five emotions having the highest weight on factor 1 are sadness, present in all three groups, curiosity, amazement, and despair, present in sighted and late blind subjects only. In

the case of the second factor, instead, all groups show a higher weight for agitation, while panic is common between sighted and early blind only, and the emotion of love is present for early and late blind.

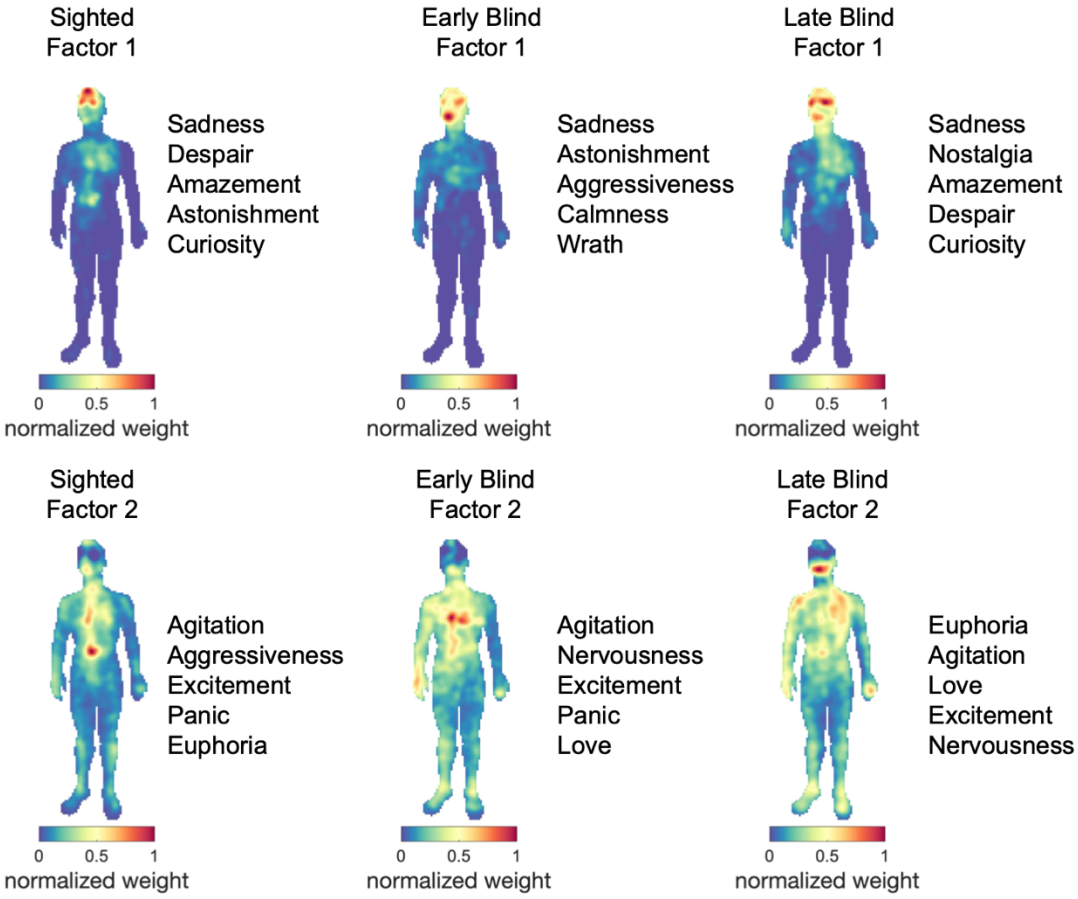


Figure 4. Low dimensional embedding of bodily maps of emotions. The uppermost part of the figure reports the bodily maps showing the expression of Factor 1 in sighted, early and late blind individuals, while the lower one is related to Factor 2. The intensity of the red color represents the higher weight of that region on the Factor. Five emotions weighing the most on each factor are reported next to each bodily map.

Discussion

In the current study, we demonstrate how the lack of vision affects how people represent emotions in the body through an ecological haptic task. By asking groups of early and late blind individuals, as well as sighted volunteers, to indicate where in the body they experience changes associated with a specific emotion, we were able to detail the impact of visual experience on the bodily representation of emotions. Our results highlight substantial differences between sighted and blind participants and point to the fact that the bodily representation of emotion is malleable and partially grounded on visual experience. Overall, blind and sighted individuals attribute different importance to specific body regions, as sighted people focus more on visceral sensations, while blind individuals give more importance to the mouth and the hand areas. Also, we observe important differences in the coherence of bodily maps of specific emotions, such as aggressiveness, for which both early and late blind are highly homogenous in reporting the mouth region, while the sighed mostly report the entire body with a focus on the chest region. Of note, this similarity within groups underscores that sighted individuals tend to share more commonalities in the way they represent emotions, while early and late blind participants also exhibit greater similarity with each other in this regard. Moreover, we find similar body regions with higher relevance extracted from the maps of our groups, especially the head area demonstrating a strong value for both sighted and blind participants. Lastly, our findings show that blind people rely on a different organization of affect, as only sighted categorize bodily maps of emotion through the valence and arousal dimensional space. Even if the onset of blindness did not affect most of the above-mentioned results, the bodily representation of emotions was however also

influenced by the period of acquired blindness, as for instance in the case of how the stomach region relates to some affective states.

The cognitive neuroscience of blindness has compellingly revealed how visual deprivation impacts various domains of behavior, perception, and cognition (e.g., Collignon et al., 2006; Cattaneo et al., 2008; Bedny and Saxe, 2016; Bottini et al., 2016). However, how the lack of sight influences affective processing is still largely unexplored, even if emotions are pervasive in our daily lives. Moreover, the body is the first instrument through which we interact and explore the external world, and bodily signals are crucial when interacting with other individuals. Several of these signals are, in fact, not accessible to blind people. Previous research has indicated that children with visual impairments often delay acquiring Theory of Mind abilities (Peterson et al., 2000; Green et al., 2004). However, recent studies have challenged previous research findings suggesting a delay in the development of social cognition among blind individuals, showing no developmental delay in advanced Theory of Mind comprehension among congenitally blind children compared to sighted peers (Pijnacker et al., 2012), or a similar performance (Bartoli et al., 2019; Richardson et al., 2023). It is important to note that all these recent studies employed more inclusive tools for assessing social cognition in visually impaired children, potentially explaining the contrasting findings with earlier research and highlighting the importance of using appropriate tools and methodologies when studying social cognition in individuals with visual impairment or blindness.

Furthermore, a recent study based on semi-structured interviews found that, in the absence of visual inputs, language plays a relevant role in pairing bodily reactions with emotions (Giraud et al., 2023). Nonetheless, the extent to which sensory experiences influence the embodiment of emotions remains relatively uncharted. In this study, we aimed

to address this pivotal question by employing visual deprivation as a model system for the representation of emotions in the body.

We demonstrate that the bodily representation of affect is grounded in sensory experience, as we observed significant differences in bodily maps of sighted and blind individuals. The responses of early and late-deprived subjects showed more similarities than differences, with the main exception being the general involvement of the stomach region. In this case, the group of late blind acts as a middle ground between sighted and early blind, suggesting that even a short amount of time passed without receiving visual inputs is sufficient to trigger a reorganization in how people perceive bodily reactions brought about by an emotion. Interestingly, how late blind are often located halfway between the perceptual and cognitive phenotype of sighted and early blind has been demonstrated in various other domains, as for instance in auditory discrimination (Gougoux et al., 2004) and categorization (Mattioni et al., 2022), spatial hearing (Collignon et al., 2013), language processing (Pant et al., 2020), pain perception (Slimani et al., 2014), and odor localization (Manescu et al., 2021).

Of note, the differences we observed in the bodily representation of emotion between sensory deprived and sighted individuals might be associated with the differing life experiences encountered by these two groups on a daily basis. Blind individuals may develop a wide range of unique strategies and mechanisms to effectively navigate and manage their emotional responses in light of the multifaceted challenges posed by their blindness. These challenges extend beyond the physical limitations imposed by their visual impairment, encompassing the complex interplay of societal attitudes, accessibility barriers, and everyday obstacles encountered in various facets of their lives. In response, blind individuals often develop an experiential adaptive dimension of disability, tailored to their specific

circumstances, drawing upon a diverse range of resources, including social support networks, assistive technologies, and psychological resilience (e.g., Boerner and Wang, 2012). These strategies not only facilitate emotional regulation in the face of adversity but also foster a sense of empowerment and agency, enabling individuals to actively engage with and overcome the challenges inherent in their lived experience of blindness. Furthermore, blind individuals undergo a profound reconfiguration of their conceptual framework concerning somatic responses to emotions, a process intricately intertwined with their reliance on haptic cues in daily life (e.g., Koutsoklenis and Papadopoulos, 2014). This recalibration suggests a nuanced understanding of emotional embodiment, where the absence of visual input prompts blind individuals to cultivate heightened sensitivity to tactile, auditory, and olfactory signals as proxies for emotional expression and recognition. The adaptive reliance on non-visual sensory modalities could underscore a distinctive construction and reconstruction of emotional experiences, fundamentally distinct from those of sighted individuals. Of note, the incorporation of haptic cues into the interpretation of emotions, reflects a dynamic interplay between perceptual, sensory, and cognitive processes, shaping a unique embodiment of emotional responses rooted in alternative parameters and indicators. Consequently, blind individuals develop a richly nuanced understanding of emotions, characterized by an intricate interweaving of tactile sensations, auditory cues, and interpersonal interactions, highlighting the multifaceted nature of emotional experience within the context of visual impairment. Overall, understanding and appreciating these differences is crucial for fostering empathy, inclusivity, and effective communication with sensory deprived individuals.

The fact that sighted participants attributed more importance than blind people to the stomach area of the body across emotional states is of particular interest. Previous animal studies have shown reduced gastric activity after visual deprivation (Schapiro et al., 1970;

1973). In humans, neuroimaging evidence has pointed out the role of the insular cortex in representing gastric and visceral activity (Critchley and Harrison, 2013; Uddin et al., 2017; Avery et al., 2017). Importantly, the brain functional connectivity of insular regions is altered in blindness, regardless of the age at onset of visual deprivation (Liu et al., 2017; Hu et al., 2022). Furthermore, there is evidence that gastric rhythm is encoded in occipital areas (Richter et al., 2017; Azzalini et al., 2019), and animal studies demonstrated the existence of anatomical projections relaying visceral information from brainstem nuclei to the lateral geniculate nucleus (Erisir et al., 1997a,b; Guillery and Sherman, 2002; Azzalini et al., 2019). Interestingly, blind individuals show a reduction in the volume of both subcortical structures like the lateral geniculate nucleus (Ptito et al., 2008; Cecchetti et al., 2016) and in occipital visual areas (Lepore et al., 2010). Considering all this, we can speculate that the alteration in insular and subcortical regions in blindness might have an impact on the perception of interoceptive signals, ultimately determining that early and, to a lesser extent, late blind, conceptualize visceral sensations associated with the experience of emotion differently from sighted people. Our findings shed light on the nuanced ways in which blind individuals perceive and interpret bodily sensations associated with emotional experiences. Indeed, when prompted to identify regions within their body linked to emotional responses, blind may prioritize or emphasize certain bodily sensations differently than sighted, due to their unique sensory experiences. For instance, while blind demonstrate proficiency in discerning interoceptive cues, particularly those arising from the heart region (Radziun et al., 2023b), this aptitude may not necessarily translate into a heightened ability to represent emotions within the body, as counting heartbeats is a purely interoceptive task and may not fully capture the complexity of emotional embodiment. Thus, while interoceptive signals may be a

prerequisite for emotional embodiment, they may not be the only relevant component to be aware of the bodily response associated with specific emotional experiences.

We also found a higher intra-group coherence in the bodily maps of specific emotions. Sighted participants again show a strong within-group reliability in reporting the stomach area for the emotion of love, even if it is observable in other states like attraction and wrath as well. Early and late blind participants, instead, are coherent in focusing on the mouth region for the emotion of aggressiveness. As observed also in the factors extracted from our bodily maps, blind individuals put more relevance to the eyes and mouth regions of the face, together with the heart and the hand. This difference points to distinct processes for the sensory-deprived and sighted subjects in recognizing and experiencing emotions in the body. Indeed, blind individuals might focus on the mouth since they rely more on the verbal expression and communication of their emotions, while the hand represents the haptic channel through which they can explore and interact with the external world. On the developmental side, early evidence showed how children with blindness used vocal means to elicit contact and often checked the presence of their mothers in the room by vocalizing (Preisler, 1991; 1995). Moreover, a recent study has demonstrated how blind individuals perceive more pleasant and prefer a touch on the palm of the hands, over the rest of the arm (Radziun et al., 2023a). It is also possible that blind people focus more on the hand as a primary way to communicate affective states to other individuals, for instance by caressing or holding someone else's hands.

Furthermore, the components extracted from our bodily maps were quite similar among our experimental groups. Specifically, for all participants, we found that the first factor is the head region, while the second one is the rest of the body. Interestingly, both sighted and blind individuals retain a distinction in emotional experiences between a more

cognitive component in the head, and states that are instead purely somatic. Moreover, for all groups, we found some correspondence in how emotional states have been arranged between head and body, as for instance sadness in factor 1 is associated with the head region in sighted and blind. On the other hand, more arousing states as agitation and excitement are reported in the whole body by all groups. This finding suggests that the sense of vision, overall, does not influence whether an emotional state holds a higher cognitive or somatic component. However, differences emerge when considering the representation of affective experiences in the body at a more specific level.

We also observed that the arrangement of emotions in the valence-arousal dimensional space is associated with bodily maps in sighted but not in the blind groups. Even if we may not be aware of it, we are used to categorizing affective experiences as positive/ negative and more or less activating (Posner et al., 2005). Our findings indicate that the dimensional organization of affect might be true for sighted individuals only, suggesting that sensory deprivation - happened early or later in life - might cause a different conceptualization and structuring of emotions, even if other unexplored factors may also play a role in this association.

In conclusion, here we demonstrate that visual experience plays a causal role in shaping the bodily representation of emotion. Indeed, sensory inputs modulate how individuals attribute relevance to different body parts in affective experiences, modify the weights of interoceptive and exteroceptive signals, and alters how emotions are conceptualized in the body. Our findings contribute to the ongoing debate regarding the embodiment of emotions, shedding light on the interplay between interoceptive signals and sensory experience, and deepening our understanding of how humans encode and represent emotions within their body. Future studies should take advantage of the approach we propose

to delve deeper into exploring alternative hypotheses and to ensure the generalizability of our findings.

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