THE NEURAL EMBODIMENT OF HUMAN EMOTION

by

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The Neural Embodiment of Human Emotion
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Colloquially, we describe emotion as something we feel, but it remains unknown whether emotional experiences and bodily sensations share representational space in the human brain. Does the neural basis of emotion include activation in cortex specialized to represent bodily sensation and action? There is growing evidence that emotions are ‘embodied,’ or grounded in simulations of some modality, such as perception and action. However, a causal link between reports of bodily sensations and discrete emotional states has not been established. This investigation aims to bridge bodily sensations of emotion with its neural construction by analyzing the representational similarity between self-reported topographical maps of emotion-induced bodily activation and neural activity in select sensorimotor and perceptual regions of interest. This exploratory investigation shows that: (1) Emotional images induce subjective sensations of bodily activation, (2) Self-reports of embodiment are correlated with physiological arousal, (3) Self-reported bodily representations of emotion are most similar to neural representations in the visual cortex, indicating that saliency, not somatization, may influence reports of embodiment. This investigation establishes a link between embodiment and physiological responding, but fails to establish a neural link between embodiment and sensorimotor representations. In summary, the relationship between emotion and the body is not purely conceptual: It is supported by physiological responses. Emotion-related bodily representations may serve to ready an organism for social or survival-related action. Knowledge of these representations may contribute to the biomarker initiative and provide neural targets for emotion regulation in the clinic.

CONTENTS

CHAPTER

TABLES

Table

FIGURES

Figure

CHAPTER I

INTRODUCTION

Significance Statement

Emotions coordinate neurobiological, physiological, and sensorimotor processes into adaptive, organism-wide responses that support survival and psychological well-being. Therefore, successful detection and treatment of emotion-related disorders hinges upon the knowledge of how emotions are represented in the brain. This investigation unlocks a piece of that puzzle by critically analyzing the contributions of sensorimotor processing in the instantiation of an emotional experience. The results provide promise that therapies targeting bodily sensations can change an emotion at a fundamental level of neural construction.

Theoretical Motivation

The human body expresses emotion and the brain instantiates it (James, 1884). This connection between brain and body, though compelling, is not as linear as it appears. Emotion theorists, dating back to Darwin have argued that our bodies are not just tools for expression and action, but instead, active participants in the emotional experience (Darwin, 1872). For example, William James proposed that the emotion itself arises only after the brain recognizes some change in the body's physiology (James, 1884). Indeed, emotions incite profuse bodily changes, including, but not limited to physiological arousal, visceral sensations, facial contortions, gestures, and action readiness (Ekman, 1993; Gelder, 2006; Levenson, 2014). Personal accounts render emotions and the body inseparable

(Damasio, 2000). When asked to recall an emotion, for example, a fit of anger, people may recount bodily sensations such as rising temperature, furrowed brows, and even a balled up fist (Niedenthal, 2007). Our language echoes this connection (Barrett, Lindquist, & Gendron, 2007). Common phrases used to express emotion have bodily referents: We experience *gut* feelings, a lump in the *throat*, hot *headedness*, shivers down the *spine*, and a sunken *heart*. Indeed, when asked to indicate on a silhouette of the human body, where one "feels" an emotion, people produce statistically separable topographic bodily sensation maps for discrete complex and basic emotional states, and these maps are consistent across Eastern and Western cultures (Lauri Nummenmaa, Enrico Glerean, Riitta Hari, & Jari K. Hietanen, 2014). Despite this profound collection of behavioral evidence for the embodiment of emotion, it remains unknown whether this relationship between brain and body is purely conceptual, or if it has a neural basis. Does the neural representation of emotion include activation in cortical regions specialized for bodily sensation and action? This investigation aims to provide a neural link for the embodiment of emotion by analyzing the representational similarity between self-reported topographic body maps of emotion and neural activation in select sensorimotor regions of interest: somatosensory, premotor, and motor cortices.

Embodied emotion is a subcomponent of grounded cognition theory, which argues that all cognition is subserved by simulation, and that both concrete and abstract knowledge representations retain some form of modality: perception (the senses), action (movement and proprioception), or introspection (mental states and affect) (Barsalou, 2008). In this framework, emotions are grounded in bodily sensations, that is, an emotional experience is dependent upon neural simulations within sensorimotor circuitry (Wilson-Mendenhall, Barrett, Simmons, & Barsalou, 2011). Clever behavioral manipulations and lesion studies support this proposal. For example, the restriction of movement influences the interpretation of emotional stimuli (Stepper & Strack, 1993). In this classic experiment, participants were required to hold a pen in between their teeth in a way which forced a smile or prevented one. Smiling participants evaluated neural stimuli as more pleasing that those who were not (Strack, Martin, & Stepper, 1988). In another investigation, posture determined emotional interpretations of a new situation: Participants sitting in an upright position reported greater feelings of pride when they were delivered good news than their slumped over counterparts (Briñol, Petty, & Wagner, 2009; Dael, Mortillaro, & Scherer, 2012). This "reciprocal relationship" between bodily expressions and the way in which emotional information is attended to and interpreted is further supported by lesion studies: Patients with right ventral primary and secondary somatosensory cortex lesions demonstrate impaired recognition of emotional facial expressions, despite having intact visual processing streams (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Niedenthal, 2007). Drawing across this evidence, embodied emotion theory purports that somatosensory and motor simulations are critical to the expression and recognition of emotional states.

The behavioral and neural evidence cited insofar rely almost entirely on self-reports and provide little to no neural evidence that representations of bodily states are intrinsic components of an emotional experience. Do these effects exist only in self-report, which can easily be biased (Nili et al., 2014) or influenced by experimental demands, or are they instantiated by neural substrate? To answer this question, this experiment interrogates the similarity between self-reported topographic maps of bodily emotion and neural representations within sensorimotor and perceptual cortices using neuroimaging and multivariate analysis techniques. In this experiment, in-lab participants viewed emotional images, that varied in valence, complexity, and content, while high temporal and spatial resolution images of their brains were collected in an fMRI scanner. Self-reports were collected after the scan, so that neural activation was not compromised by experimental demands such as cognitive appraisals or button responses. Representational similarity analysis was used to compare the representation of emotional content at four levels of analysis: embodiment reports, cognitive appraisals, physiological responses, and neural activity (Nili et al., 2014).

CHAPTER II

MATERIALS AND METHOD

Participants

Participants (N=18) were recruited from the University of Colorado-Boulder and the surrounding community (10 Female, Average Age = 25, right-handed). Participants did not meet DSM V criteria for psychological disorders, had no life history of head trauma, nor any contraindications for the MR environment, meaning their bodies were free of ferromagnetic substances.

Study Design

Picture stimuli were selected from the International Affective Picture System System (IAPS) and the Geneva Affective Picture Database (GAPED) using published normative arousal ratings, so that each image was selected to be of high arousal and belonged to a predetermined category of appraisal (see Table 1) (Dan-Glauser & Scherer, 2011; Lang, Bradley, & Cuthbert, 2008; Libkuman, Otani, Kern, Viger, & Novak, 2007; Mikels et al., 2005). 112 images were used in this experiment. Images were presented while the subject was lying in the scanner. Image presentation lasted 4-seconds, with a randomized jittered inter-trial-interval of 2 to 12-seconds (average ISI time per run = 4-sec). The image presentations were divided into two 7.5 minute runs, where the first 56 images were presented in a randomized order, followed by a random presentation of the remaining 56 images. The MATLAB Psychtoolbox package was used for the stimulus presentation. Skin conductance responses were recorded throughout the task (BIOPAC systems). Scans were acquired using a multiband imaging protocol with a 460 ms TR on a Siemens 3-T. Distortion correction scans were collected for multiband image preprocessing.

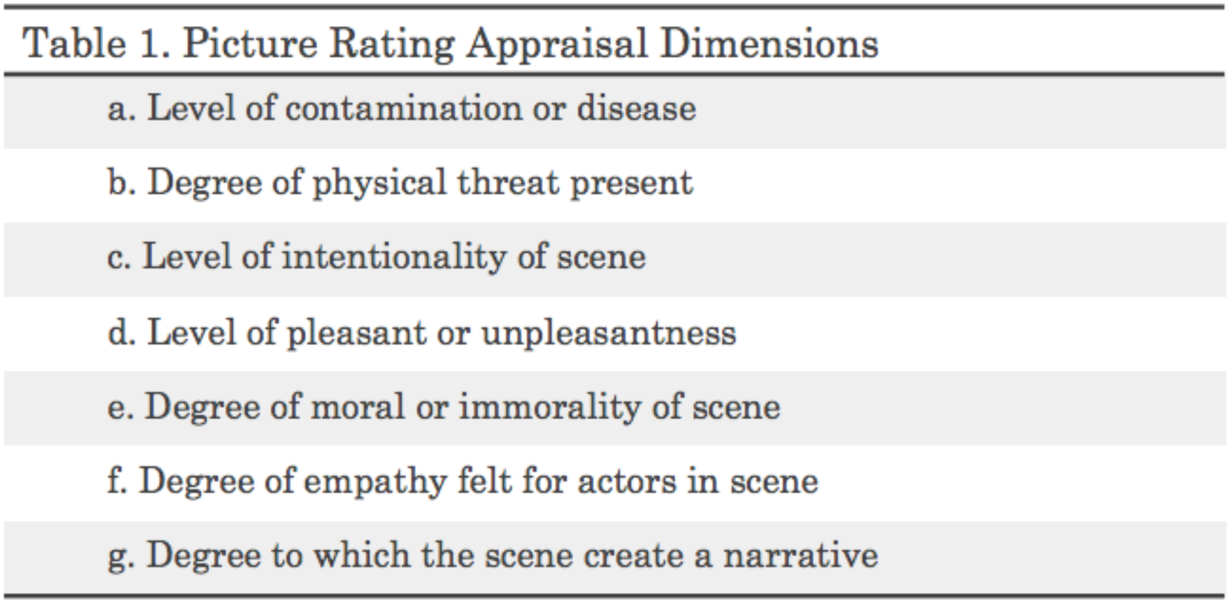

Table 1. Picture Rating Appraisal Dimensions
a. Level of contamination or disease
b. Degree of physical threat present
c. Level of intentionality of scene
d. Level of pleasant or unpleasantness
e. Degree of moral or immorality of scene
f. Degree of empathy felt for actors in scene
g. Degree to which the scene create a narrative

Table 1. Participants rated each IAPS image on the seven different appraisal dimensions listed here.

In order to control for motor-response tendencies and meta-awareness of one's appraisals, appraisal ratings were collected after the scan. In this rating session, the subject was shown the images again, in the same order presented to them during the experiment. Each image was rated on the seven predetermined appraisal dimensions (see Table 1). Ratings were given on a visual analogue scale with the anchors (NOT AT ALL and EXTREMELY SO). Participants could mark anywhere on the scale and submit their rating with a click. Ratings were encoded using a 1 - 100 scale. Participants were also asked to color on a body map (Figure 1), where, if at all, they experience a response to the image in their body. Body map reports were encoded in a binary fashion (on or off, by pixel). This post-experiment rating survey was delivered using MATLAB Psychtoolbox.

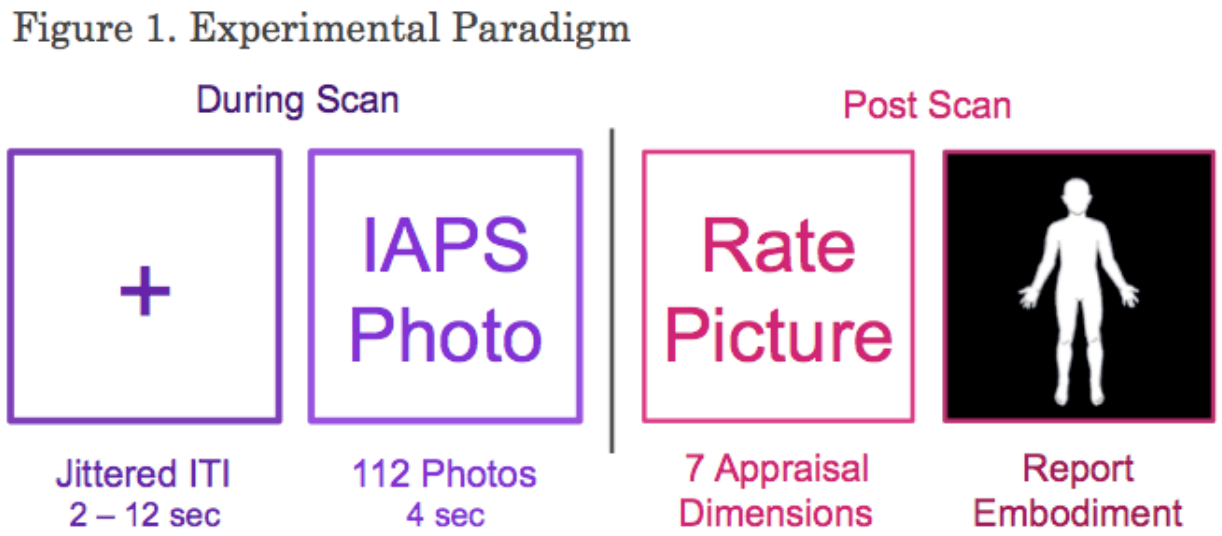

Figure 1. Participants viewed emotion-inducing images while in the fMRI. Images were rated on seven appraisal dimensions outside of the MRI. Participants also reported embodied sensations in response to the images on a silhouette of a human body.

Analysis

Body Map Preprocessing. Single trial binary self-reported bodily activation maps were reduced in dimensionality to 200 x 100 pixels and then smoothed using a radial dilation (5 pixel diameter, Figure 2). Radial dilation allowed for graded activation in pixel, in a range of 0 to 1. Body maps were vectorized, meaning each pixel activation value was stacked into a single vector in a meaningful order, for further analysis.

Figure 2. Preprocessing of Body Map Data

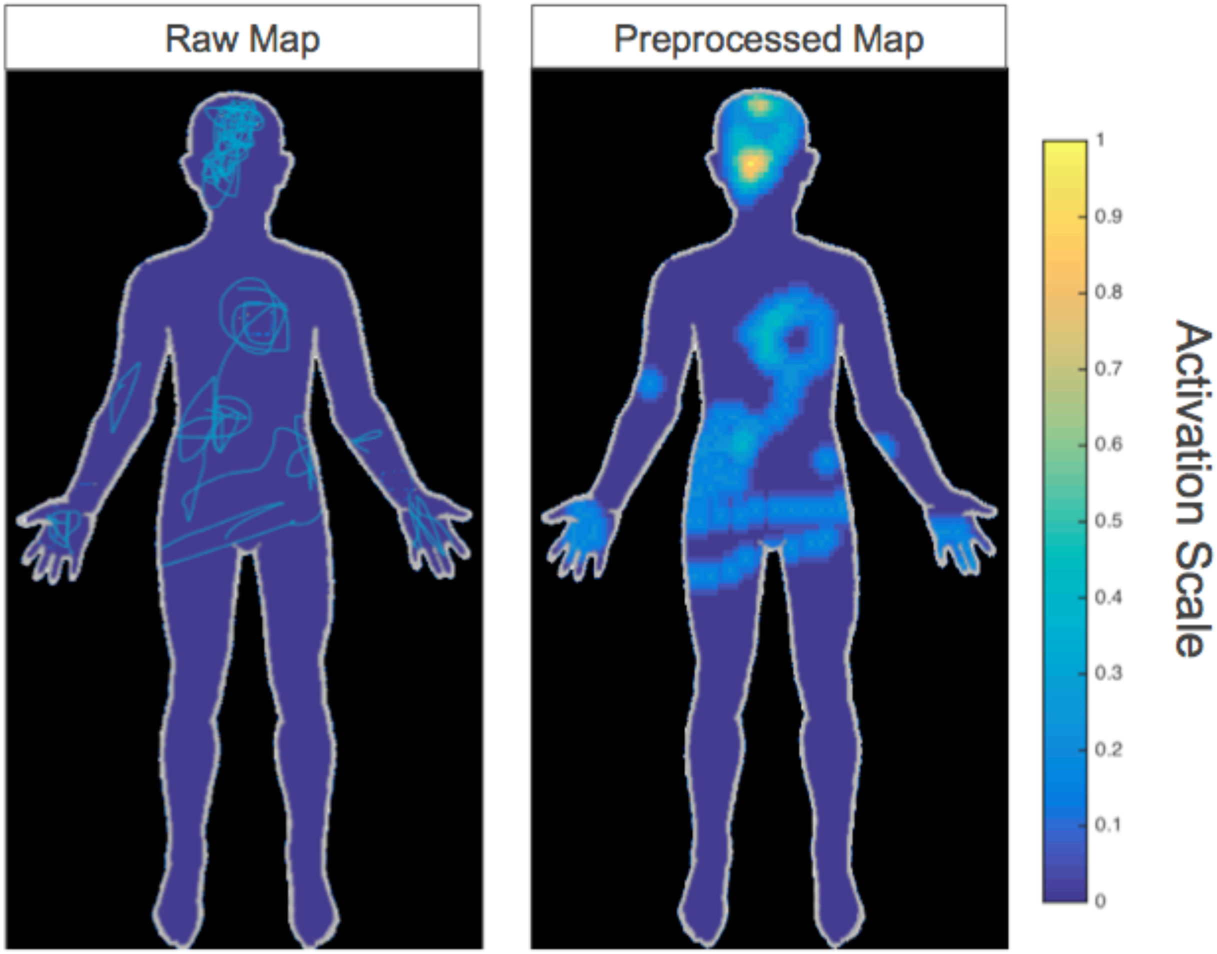

Figure 2. Example of raw (left, completed by subject during the task) and preprocessed (right, dilated) body map data from a single trial of a single subject.

Skin Conductance Response (SCR) Preprocessing. SCRs were collected at 1000 Hz sampling rate. Traces were low pass filtered using a 200 Hz Butterworth filter and then smoothed by a sliding window with a factor of 3. Event-related SCRs were collected using Ledalab continuous decomposition analysis to assess the phasic amplitude of the response, above slow tonic changes. Trace SCRs were collected by extracting the event-related SCR time series, per trial, per subject.

Multiband Neuroimaging Preprocessing. Multiband neuroimaging data were preprocessed using the Human Connectome Project preprocessing pipeline which includes distortion correction, motion correction with 24 parameters, spatial normalize via the subject's native T1 image, and a smoothing factor of 6mm (Glasser et al., 2013). A combination of in-house software, FSL, and SPM were used.

Neuroimaging First-Level Univariate Analysis. Events were modeled using a single-trial general linear model, where one regressor was included for every stimulus image, for a total of 112 regressors per subject. In house software and SPM were used.

Neuroimaging Region of Interest (ROI) Analysis. Bilateral anatomical sensorimotor and perception ROIs were determined a prioi, and selected from the Hard-Oxford Anatomical Atlas. A 50% probabilistic threshold was applied. These ROIs were the primary somatosensory cortex (S1), primary motor cortex (M1), supplementary motor area (SMA), insular cortex, and the occipital pole (visual cortex, Figure 3). These masks were applied to the univariate beta weight maps of each subject, to each image, and the voxel-wise activation patterns were extracted for further analyses.

Figure 3. Embodiment Regions of Interest

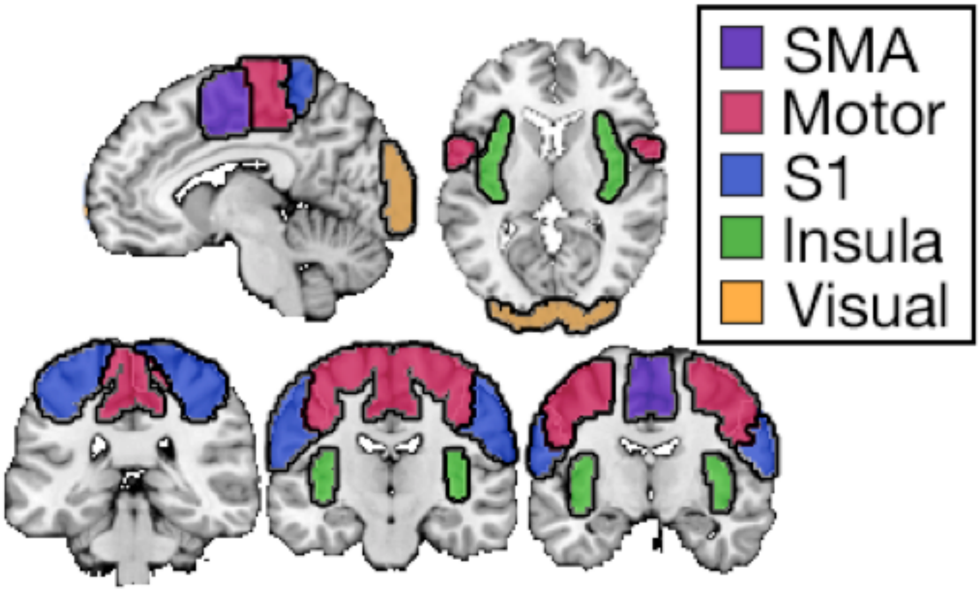

Figure 3. Depiction of the structural anatomical masks for the five sensorimotor and perceptual embodiment regions of interest used in this analysis.

Representational Similarity Analysis (RSA). The goal of this RSA is to map four forms of emotion representation: neural (5 ROIs), physiological (SCR), bodily sensation, and cognitive appraisal (subjective ratings of the emotional content of the image), into the same 'emotion space' so that the representational content of each different measure can be directly compared.

First-Level. Single-trial ROI voxel patterns, vectorized body maps, vectorized appraisal ratings (participants made seven appraisal for each image, their scores were input into a 7x1 dimensional vector, one per trial), and SCR traces were used in this analysis. For each of these measures, a subject-specific representational dissimilarity matrix (RDM) was constructed by taking the one minus the Pearson's correlation between every trial, so that 112x112 confusion matrix resulted for each measure (5 ROIs, body maps, appraisals, and SCRs) for each subject (Figure 4). Subject-specific RDMs were normalized using a Fisher R to Z transformation.

Figure 4. Illustration of RSA Procedure for ROI Activity Patterns

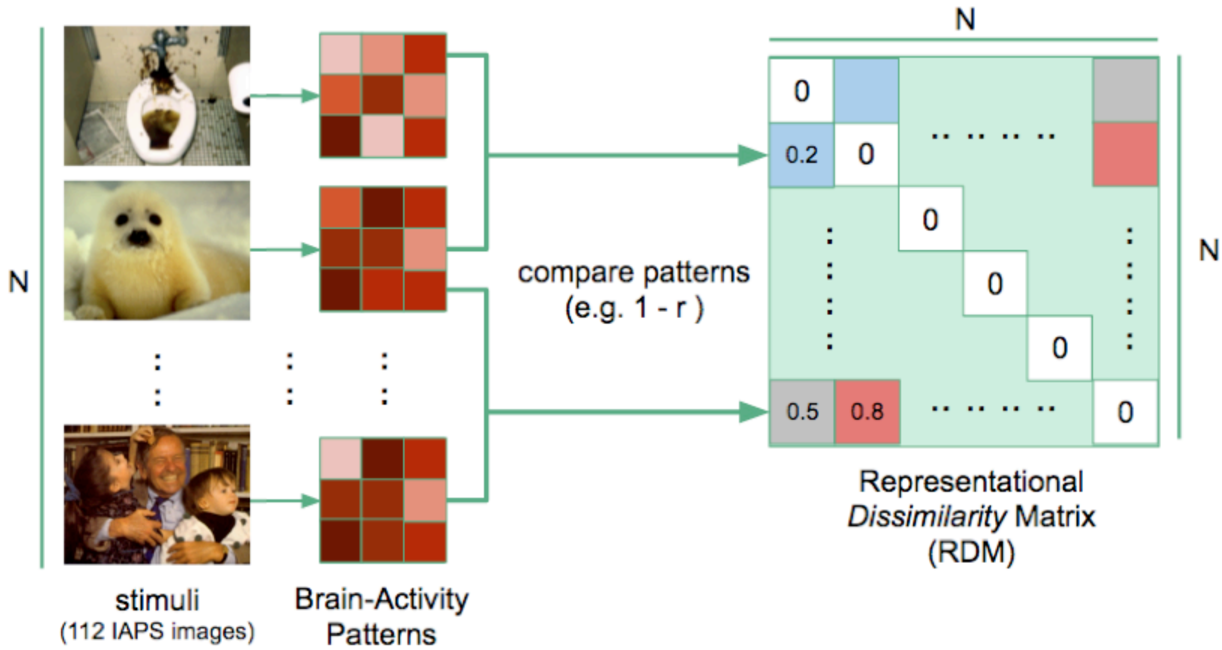

Figure 4. At the first-level, the RSA procedure takes voxel-wise activity patterns within an ROI of a single subject to each stimulus image. Voxel-wise activity patterns are compared using 1 minus Pearson's correlation. The resulting coefficient is entered into correlation matrix that represents the degree of dissimilarity of stimulus image representations within the ROI. This procedure is

repeated for each subject, at each level of analysis (brain, physiology, and self-report). This image was adapted to fit this investigation from Nili et al. (2014).

Second-Level. RDMs were then averaged in the third dimensions across subjects within the eight emotion measures of interest, so that there were eight second-level RDMs: one for each emotion measure: physiology, bodily sensation, appraisal ratings, and neural activation in the five ROIs. Averaged RDMs were then entered into multidimensional scaling and hierarchical clustering algorithms for more descriptive graphical representations.

RDM Comparison. The second-level RDMs were then vectorized and correlated together using Spearman's rank correlation, so that the different representational spaces of emotion could be compared. This final RDM was then entered into multidimensional scaling and hierarchical clustering algorithms for more descriptive graphical representation.

CHAPTER III

RESULTS

Evidence for Embodiment

Emotional images induced a subjective sense of emotion embodiment in 14 out of 18 participants. 4 participants did not report embodiment, meaning they chose to leave the body maps blank for all 112 IAPS images.

RDMs of Emotional Content.

The purpose of this analysis is to assess commonalities between representations of the emotional content of the experimental stimuli across eight different levels of analysis: Cognitive Appraisals, SCR (Physiology), Body Maps, and the five ROIs. The 112 visual stimuli were reordered according to valence and content, as determined by published normative ratings (Lang et al., 2008; Mikels et al., 2005). The ordering ranged from negative (violence, contamination, inhumane treatment of people and animals, and self-directed threats) to positive (comforting images of children and baby animals, romantic couples, positive social interactions, nature, sex, and appetizing food) images. This order was consistent across analyses in order to make it easier to differences in representation according to valence within the RDMs. For example, if quadrants are visible in the RDM, then the representation of emotion is influenced by valence in that level of analysis. Correlational weights in the RDMs were then input into a hierarchical clustering algorithm, which, in an unsupervised manner, clustered the stimuli according to representational similarity. Linkage was determined by a weighted average. The purpose of this clustering is purely descriptive, as it may reveal relationships between stimulus representations that are not readily noticeable in the RDM itself due to the fixed ordering of the stimuli.

Appraisal RDM. Cognitive appraisals revealed a clear representational space of emotional content based on valence (negative content separable from positive content). This separation was expected: The appraisal ratings which went into this analysis were, contamination, threat, intentionality, pleasantness, morality, empathy, and strength of narrative, and therefore provided an assessment of valence, which correspond to the normative ratings the images were ordered by (Figure 5A).

Figure 5. Second-Level RDM
A) Appraisal Space RDM & Dendogram

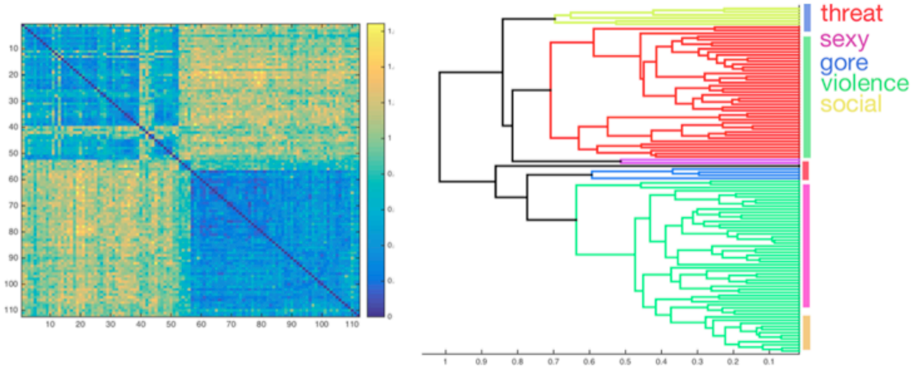

Figure 5A. Second-Level RDM of the Emotion Space of Appraisal Ratings. RDM (left) shows an emotion space determined by valence of stimulus content. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM.

SCR RDM. At the second level, physiological responses were clustered into two discernable categories of emotional content: highly arousing positive (erotic) and highly arousing negative (violence and gore) images. Images of low arousal or low saliency were not clustered in a discernable way. This indicates that highly salient emotional content is represented in SCR in a manner sensitive to valence (Figure 5B).

Figure 5. Second-Level RDM
B) Physiology (SCR) RDM & Dendogram

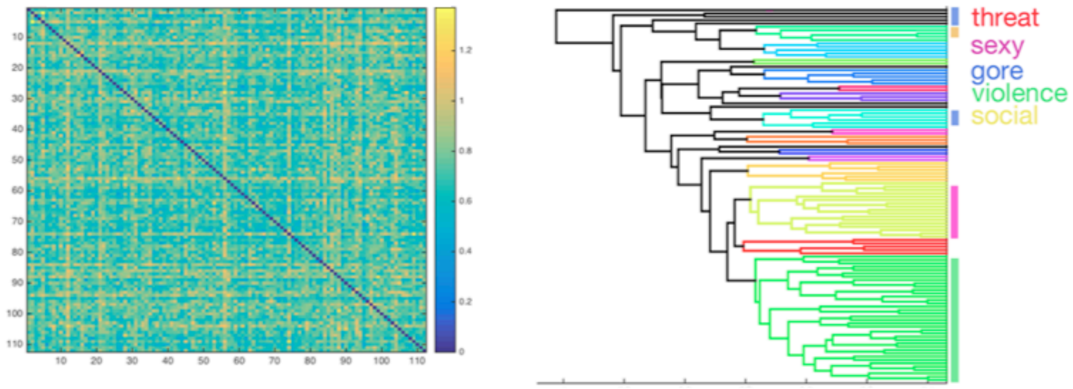

Figure 5B. Second-Level RDM of the Emotion Space of Physiological Responses. RDM (left) shows an emotion space determined by SCRs. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and indicate that emotion in SCR is organized by stimulus content, specifically violence and erotica are distinguishable from other types of stimuli.

Body Map RDM. At the second level, body maps were clustered according to four discernable categories of emotional content: threat, gore, violence, positive sociality, and sexual content. This indicates that the emotional content represented in self-reported body maps is organized by more specific emotional content than cognitive appraisals or physiology, which were grouped largely by valence and arousal (Figure 5C).

Figure 5. Second-Level RDM
C) Body Map RDM & Dendogram

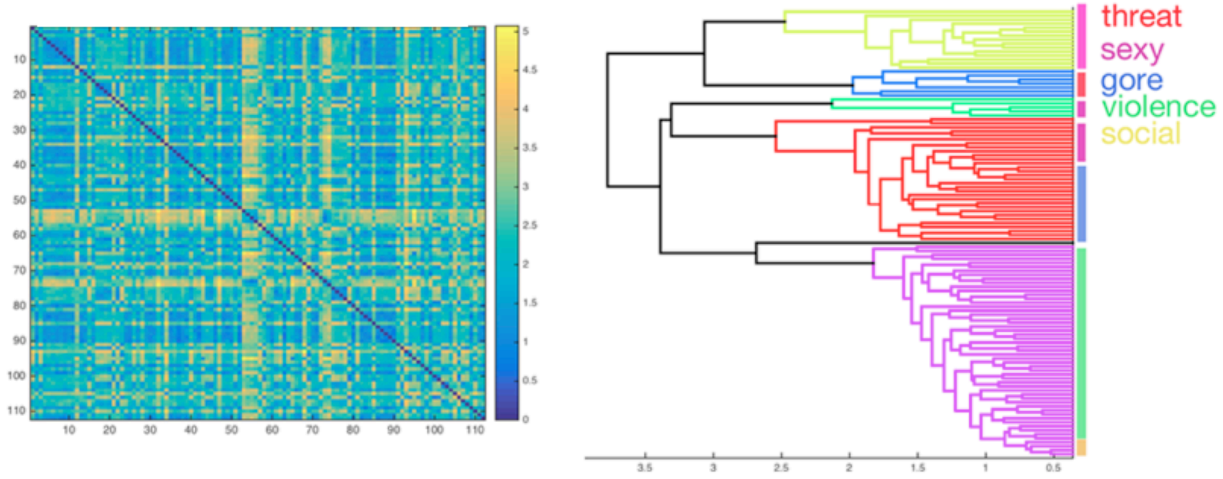

Figure 5C. Second-Level RDM of the Emotion Space of Body Maps. RDM (left) shows an emotion space determined by self-reported bodily sensations on the body maps. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM.

ROI RDMs. At the second level, visual cortex represented emotional content of nearly all the images in a similar way, however, particularly salient threatening and gory images were separable from the others (Figure 5D). Motor cortex was the most discerning of the ROIs (Figure 5E). Emotional content was clustered into three separate categories: violence, gore, and sex. No discernable organization of emotional content was uncovered in the SMA (Figure 5F), S1 (Figure 5G), or Insula (Figure 5H).

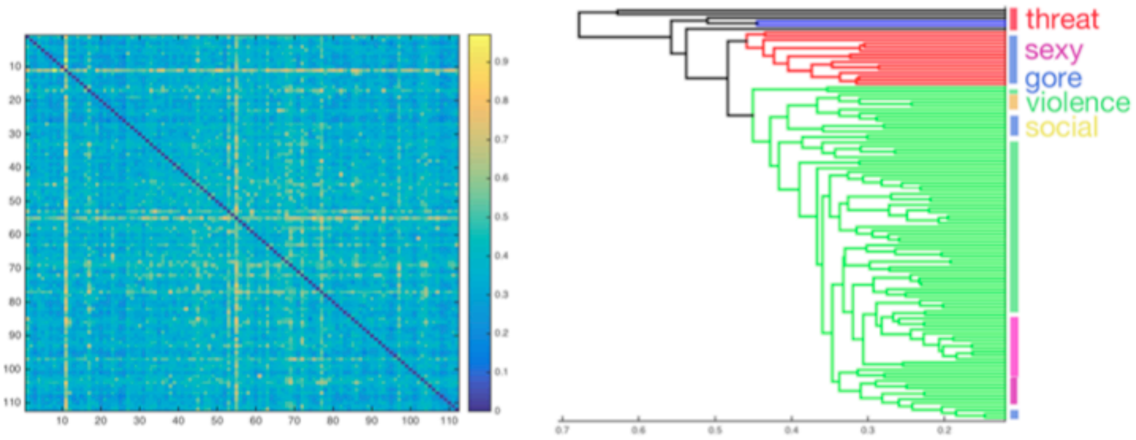
Figure 5. Second-Level RDM
D) Visual Cortex ROI RDM & Dendogram

Figure 5D. Second-Level RDM of Visual Cortex ROI. RDM (left) shows an emotion space determined by voxel-wise activation patterns in the visual cortex. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and indicates that stimulus saliency may be the organizing factor.

Figure 5. Second-Level RDM
E) Motor Cortex ROI RDM & Dendogram

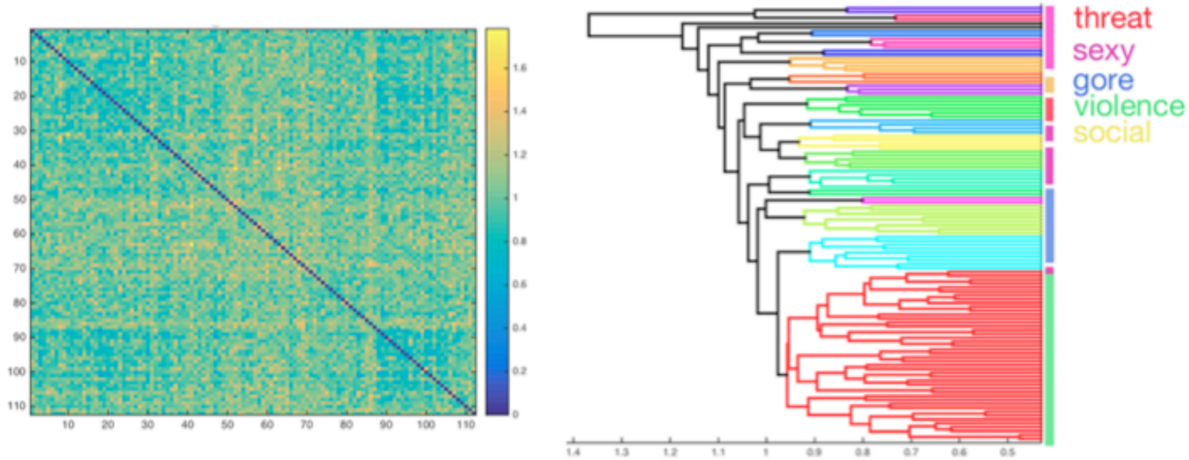

Figure 5E. Second-Level RDM of Motor Cortex ROI. RDM (left) shows an emotion space determined by voxel-wise activation patterns in the motor cortex. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and indicates that stimulus content is organized possibly by action readiness.

Figure 5. Second-Level RDM
F) SMA ROI RDM & Dendogram

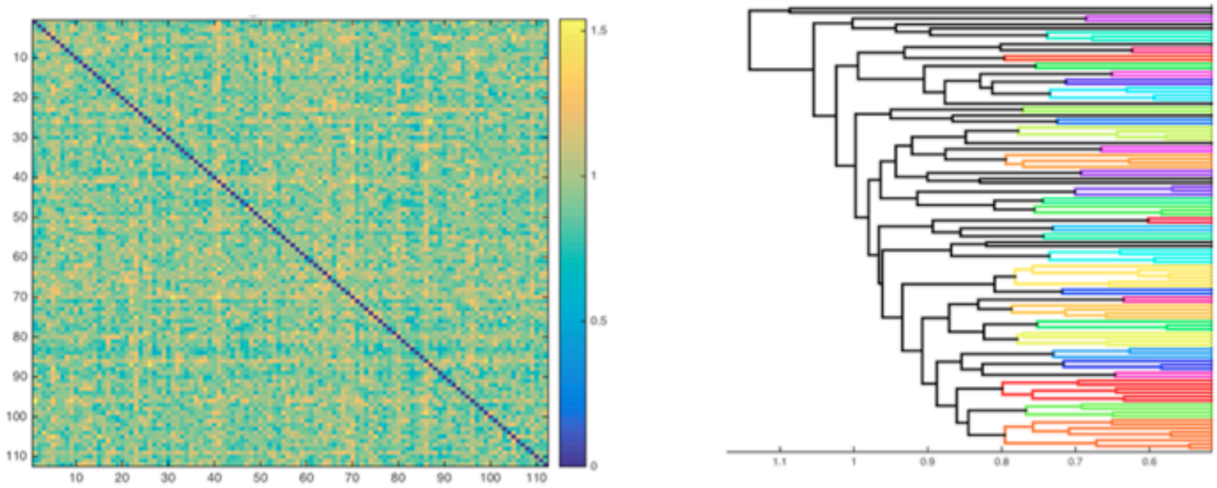

Figure 5F. Second-Level RDM of SMA ROI. RDM (left) shows an emotion space determined by voxel-wise activation patterns in the SMA. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and reveal no organization of stimulus content.

Figure 5. Second-Level RDM
G) S1 ROI RDM & Dendogram

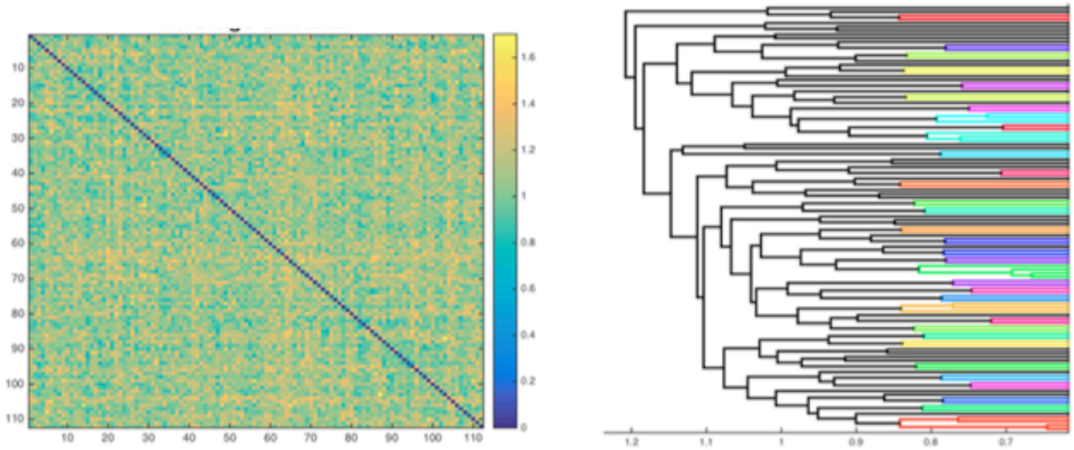

Figure 5G. Second-Level RDM of S1 ROI. RDM (left) shows an emotion space determined by voxel-wise activation patterns in S1. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and reveal no organization of stimulus content.

Figure 5. Second-Level RDM
H) Insula ROI RDM & Dendogram

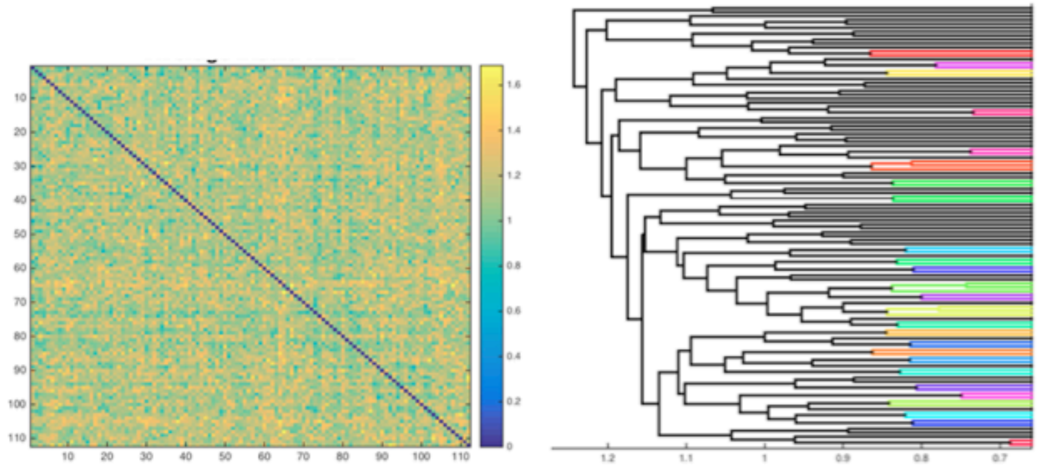

Figure 5H. Second-Level RDM of Insula ROI. RDM (left) shows an emotion space determined by voxel-wise activation patterns in the Insula. Dendogram (Right) is a descriptive depiction of the distance metrics in the RDM, and reveal no organization of stimulus content.

Comparisons of RDMs of Emotion. The purpose of this analysis is to assess commonalities between how emotional content is represented at different levels of perception and analysis, so that self-reported sensations of bodily activation can be directly compared to actual physiological and neurobiological representations of emotion. Second-level RDMs were vectorized and analyzed for representational similarity using Spearman's rank correlation (Figure 6A). Significant similarity was found between the representations of emotional content in the visual cortex and SCR ($r=0.067, p<0.05$), cognitive appraisals ($r=0.056, p<0.05$), and the body maps ($r=0.120, p<0.05$). A significant similarity was also found between the representations of emotional content in SCR and the body maps ($r=0.005, p<0.05$), while significant dissimilarity was observed between SCR and Insula cortex representations ($r=1.07, p<0.05$). Each brain ROI was significantly correlated with each other, indicating coordination across distributed regions of neural activation during the instantiation of emotion.

An unsupervised hierarchical clustering analysis (Figure 6B) and multidimensional scaling characterization of the comparison RDM (Figure 6C) revealed that the representation of emotional content is most similar between body maps, SCR, and the visual cortex. A relationship between the body maps and the sensorimotor regions of interest was not found.

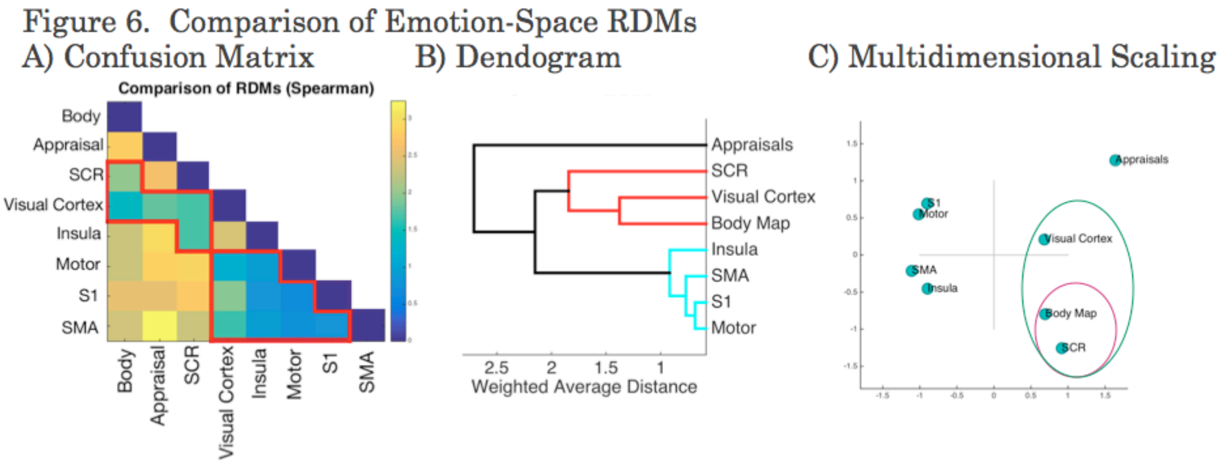

Figure 6. Comparison of Emotion-Space RDMs. **A)** This final comparison of the second-level RDMs for each measure of emotional content reveals significant similarity between the representational organization of emotional content in the visual cortex, body maps, and SCR**. B)** The Dendogram and **C)** Multidimensional scaling plots are a descriptive depiction of the distance metrics in the RDM.

CHAPTER IV

DISCUSSION

This investigation replicated the phenomenon of the subjective somatotopic sensation of emotion, but failed to establish a neural link between self-reports of embodiment and sensorimotor neural representations. However, this analysis did reveal a substantial link between reports of embodiment and emotion-related physiological responses. It is possible that when an individual recognizes a physiological change in his or her body within an emotional context, they are inclined to report bodily sensations, independent of an actual somatization. The link between physiology and embodiment is interesting because physiological responses of emotion are typically considered nonspecific. Indeed, it is thought that skin conductance reflects changes in attention and arousal, independent of valence or other dimensions of emotion (Christie & Friedman, 2004). However, the majority of studies which analyze physiology do so in an event-related fashion and extract only the amplitude of the signal at each time point of interest. This severely reduces the amount of information contained in the signal. In this analysis, the entire SCR trace following a stimulus presentation was taken, allowing us to analyze more nuanced information contained in the signal. This result supports that skin conductance responses alone can represent diverse emotional content such as valence, arousal, and situational complexity, and that physiological changes interact with subjective sensations of emotion embodiment.

Of the neural regions investigated in this study, representational content in the visual cortex was most similar to that of the body maps. One possible interpretation of this finding is that emotional saliency is influencing both visual processing and self-reports. Salient images yield greater attentional demand, which, in turn, enhances stimulus processing in the visual cortex (Bradley et al., 2003). Increased saliency may also bias participants to report more embodiment, and induce a correlation between visuoattentional processing and self-reports of embodiment that may be independent of actual somatization. Participants were not forced to report embodiment, and it was considered meaningful when a participant chose to report no embodiment by leaving a blank body map on any given trial. Blank maps were included in this analysis for participants who engaged in the embodiment task and reported embodiment in at least one trial. Therefore it is possible that blank maps indicate lack of task engagement rather than lack of embodiment, or vice versa.

Another interpretation is that emotional content is represented in the visual cortex, and that this representation coincides with the body maps. There is growing evidence that IAPS images can be discriminated in visual cortex, for example, the visual cortex is amongst the most discriminatory brain regions in the IAPS-trained neural signature of negative emotion developed by Chang et al (2015), the picture-induced negative emotion signature, or PINES (Mourão-Miranda et al., 2003); (Chang, Gianaros, Manuck, Krishnan, & Wager, 2015)). This perspective is supported by grounded cognition theory, which presupposes simulations in perceptual as well as sensorimotor cortices, however, the current investigation cannot disentangle these opposing hypotheses because only visual stimuli were used in this investigation, attentional demands, and scene complexity were not measured.

The present investigation provides evidence against the notion that embodiment is a product of language or high-level construal: Embodiment could not be explained by cognitive appraisals. The emotion space of appraisal was, in fact, the greatest outlier in this analysis, as it did not map onto any of the selected brain regions or physiology. The emotion space of appraisal best captured positive and negative valence, and possibly did not capture more complex aspects of emotion representation, and therefore, was a poor fit for the other levels of analysis considered here.

Despite the failure to link the body maps to sensorimotor representation, the contributions of motor simulations to the instantiation of an emotional experience cannot be ruled out. Indeed, this investigation found evidence of embodiment in the primary motor cortex, however, these findings simply did not map onto the self-report data. Primary motor cortex activates significantly to emotional images in this task. Motion was rigorously controlled for in the first-level regression analysis, and participants were carefully instructed to remain still for the entire imaging session, which was relatively short: 14 minutes total. Furthermore, the emotion space constructed from voxel activation patterns in the motor cortex alone demonstrated an organization of stimulus content by emotional qualities such as valence and intensity. However, these representations did not correlate with self-reported embodiment. This might be due to a relative disconnect between actual motor simulations supporting emotion embodiment and what people think they are simulating. Taken together, these findings indicates that motor simulations may be important for the recognition and expression of emotion, but a person may not necessarily have conscious awareness of these simulations.

It is important to recognize that the present study is severely limited by a small sample size (N=18) and sparse self-report data. Of this small sample, only 14 participants reported any embodiment, and even in this sample, fatigue while completing the post-experiment survey is a concern. A follow up, large-scale, online investigation will employ collaborative filtering to reinterrogate these neural responses in more robust way. Collaborative filtering is using large amounts of data to make prediction on any given individual. These data will be collected online and applied to individual brains. In this way, emotion spaces based on self-report will be more reliable and powerful when applied to the neural data.

In summary, the relationship between emotion and the body is not purely conceptual: It is supported by physiological responses and perceptual representations. Human emotion is a complex phenomenological experience instantiated by neurobiological and psychological processes that include interactions between the brain and body. This investigation provides evidence that the experience of emotion cannot be isolated from experiences with the world and internal states; instead, emotion emerges from dynamic and distributed representations activated throughout the brain and body. Emotion-related bodily representations may serve to ready an organism for social or survival-related action. Knowledge of these representations may contribute to the biomarker initiative and provide neural targets for emotion regulation in the clinic.

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