

ORIGINAL ARTICLE

Computation-Based Feature Representation of Body Expressions in the Human Brain

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Abstract

Humans and other primate species are experts at recognizing body expressions. To understand the underlying perceptual mechanisms, we computed postural and kinematic features from affective whole-body movement videos and related them to brain processes. Using representational similarity and multivoxel pattern analyses, we showed systematic relations between computation-based body features and brain activity. Our results revealed that postural rather than kinematic features reflect the affective category of the body movements. The feature limb contraction showed a central contribution in fearful body expression perception, differentially represented in action observation, motor preparation, and affect coding regions, including the amygdala. The posterior superior temporal sulcus differentiated fearful from other affective categories using limb contraction rather than kinematics. The extrastriate body area and fusiform body area also showed greater tuning to postural features. The discovery of midlevel body feature encoding in the brain moves affective neuroscience beyond research on high-level emotion representations and provides insights in the perceptual features that possibly drive automatic emotion perception.

Key words: body, emotion, fMRI, movement, posture

Introduction

It is widely agreed that humans and other primate species are experts at recognizing emotion and intention from face and body expressions (de Gelder 2006; Giese and Rizzolatti 2015). The central importance of nonverbal communication across many social species suggests that the brain is equipped for rapid and accurate face and body movement perception; yet, the mechanisms underlying this ability are still largely unclear. Previous research on face and body expressions has predominantly searched for brain correlates of symbolic emotion categories (Lindquist et al. 2012; Kirby and Robinson 2017), disregarding the visual features that drive movement and emotion perception (e.g., kinematic and postural body features). This is in part due to the fact that methods for fine-grained description of body

movements were not yet available. This study used computational descriptions of body expressions to investigate which features drive emotion and body perception and how they are encoded in the brain.

Previous behavioral and computational studies have provided some indications about relevant features of body posture and movement, and their relation to emotional expressions (De Meijer 1989; Wallbott 1998; Roether et al. 2009; Kleinsmith and Bianchi-Berthouze 2012; Piana et al. 2014; Patwardhan 2017). Some important postural features have been identified, including elbow flexion, associated with the expression of anger, and head inclination, typically observed for sadness (Wallbott 1998; Coulson 2004; Vaessen et al. 2018). Other form-related features that have been investigated are the vertical extension of the

body (e.g., upper limbs remain low for sadness but high for happiness), the directionality of the movement (e.g., angry bodies are usually accompanied by a forward movement), symmetry (e.g., the movement of the upper limbs tends to be symmetrical when experiencing joy), and the amount of lateral opening of the body (e.g., hands are close to the body during fear and sadness while extended in happiness) (Kleinsmith and Bianchi-Berthouze 2012). The use of point-light displays, where the only form information is derived from motion-mediated structural cues (Johansson 1973), has been crucial in revealing the strong impact that movement kinematics, such as velocity and acceleration, have on the recognition of emotion from arm (Paterson et al. 2001; Pollick et al. 2001; Sawada et al. 2003) and whole-body movements (Roether et al. 2009).

A central, yet unanswered, question is the relation between candidate features and brain processes. There is sparse evidence in the literature on how particular features may be related to brain processes. One classical proposal is the two-stream model of visual processing with two separate brain pathways for form and movement information (Vaina et al. 1990; Giese and Poggio 2003; Milner and Goodale 2006, 2008). From the primary visual cortex, the dorsal stream leads to the parietal lobe and is specialized in localizing objects in space, processing motion signals and in the visual-spatial guidance of actions. The ventral stream leads to the temporal lobe and is responsible for visual form processing and object recognition. Two areas in this pathway have been identified that sustain a certain level of specialization in the processing of whole bodies and body parts: the extrastriate body area (EBA) in the medial occipital cortex, and the fusiform body area (FBA) in the fusiform gyrus (Downing et al. 2001; Peelen and Downing 2005; Schwarzlose et al. 2005). However, their respective functions are not yet clear and it is also not clear how they, alone or together, contribute to body expression perception.

In addition, body shape and movement elicit a widespread neural response beyond the visual analysis of body features in body-category selective areas (de Gelder 2006; Van den Stock et al. 2011), triggering processes related to their affective content, the conveyed action and for the preparation of an appropriate behavioral response (de Gelder et al. 2004; Van den Stock et al. 2011). For example, ALE meta-analyses have shown that the observation of emotional expressions involves the activity of several areas including the dorsal and ventral medial prefrontal cortices, orbitofrontal cortex, anterior cingulate cortex (ACC), posterior cingulate, insula, presupplementary motor area (pre-SMA) and temporal pole, and also of subcortical areas including the ventral striatum, amygdala, thalamus, and hypothalamus (Kober et al. 2008; Dricu and Frühholz 2016).

Besides body-category and emotional representation areas, the observation of body postures and movements strongly activates the so-called “action observation network” (AON). This network has been suggested to play an important role in the understanding of other people’s actions and their underlying intentions (Jellema et al. 2000; Rizzolatti et al. 2001; Fogassi et al. 2005; Iacoboni et al. 2005). It comprises the ventral premotor/caudal inferior frontal gyrus complex (PMv/cIFG), the supplementary motor area (SMA), the posterior superior temporal sulcus (pSTS), and the inferior parietal lobule (IPL) (Grafton et al. 1996; Decety et al. 1997; Buccino et al. 2001; Caspers et al. 2010). Recent work has also involved this network in the processing of body expressions. Specifically, higher activity has been reported in several nodes of the AON for emotional body actions as opposed to neutral ones (Grèzes et al. 2007;

Pichon et al. 2009; Kret et al. 2011a, 2011b). Recent transcranial magnetic stimulation (TMS) studies have directly implicated both the IPL (Engelen et al. 2015) and the pSTS (Candidi et al. 2011) in the recognition of fearful body expressions. Interestingly, the pSTS also appears to be involved in processing body motion cues (Grossman et al. 2010).

While studies of category representation, action, and emotion have provided evidence that the brain is endowed with social perception skills, none of them has yet raised the issue of the actual visual characteristics that drive body expression perception. The present study is the first effort to discover which specific postural and kinematic features could be computed from affective whole-body movement videos and be related to brain responses. By means of representational similarity multivoxel pattern analysis techniques, we investigated whether the (dis)similarity of body posture and kinematics between different emotional categories could explain neural responses to body expressions in and beyond body-selective regions.

Materials and Methods

Participants

Thirteen healthy participants (mean age = 25.8; age range = 21–30; three males) took part in the experiment. All participants had normal or corrected-to-normal vision and a medical history without any psychiatric or neurological disorders. All participants provided informed written consent before the start of the experiment and received vouchers or credit points after their participation. The experiment was approved by the Ethical Committee at Maastricht University and was performed in accordance with the Declaration of Helsinki.

Stimuli

Sixteen video clips of 1 s duration at 25 frames/s (i.e., total of 25 frames) were used in this experiment. Each video depicted a male actor performing an emotional body movement in an angry, happy, fearful, or nonemotional (e.g., coughing, pulling the nose, or walking) manner. Thus, each of the four movement categories consisted of four different videos. All actors were dressed in black and their faces were blurred with a Gaussian filter to avoid triggering facial perception processes. The movements were filmed against a green background under controlled lighting conditions. The resulting clips were computer-edited using Ulead and After Effects. The videos used in this experiment were selected from a larger validated stimulus set to ensure high recognition accuracy (>80%). Detailed information regarding the recording and validation of these stimuli can be found in Kret et al. (2011b).

Feature Definition

We estimated each actor’s joint positions using the state-of-the-art 2D pose estimation library OpenPose (v1.0.1; Cao et al. 2017; see [Supplementary Materials](#) for more information on pose estimation) and subsequently derived several quantitative body features, given their relevance in previous work (for a review, see Kleinsmith and Bianchi-Berthouze 2012). These features were computed in the same manner as in Poyo Solanas et al. (2020) using custom code in MATLAB (vR2017a, The MathWorks Inc.). Body features representing kinematic information comprised velocity, acceleration, and vertical movement. Postural features

Table 1 Feature definition

Kinematic	Velocity	Euclidean distance in pixel space of each keypoint between contiguous frames.
	Acceleration	Difference in velocity between adjacent frames for each keypoint.
	Vertical movement	Difference in y-axis pixel coordinates of each keypoint between adjacent frames.
Postural	Limb angles	Angle between two adjacent body segments, including the angles for the elbows, knees, shoulders, and hips.
	Symmetry	Euclidean distance in pixel space between each pair of joints (i.e., one on the left side, the other on the right) with respect to the axis that divides the body vertically by the nose.
	Shoulder ratio	Amount of extension of the body joints with respect to the shoulders (measured as Euclidean distance in pixel space).
	Surface	Surface area spanned by the total body extension in the x-axis and the extension in the y-axis (measured as Euclidean distance in pixel space).
	Limb contraction	Average of the Euclidean distances in pixel space between the wrists and ankles to the head.

Notes: (1) Each feature was initially calculated for each frame, although the time information was later averaged. (2) The features reflect spatial displacement of the body movement rather than muscular activity.

included limb angles, symmetry, shoulder ratio, surface, and limb contraction. For an overview of the feature definition procedure, see [Table 1](#). Initially, each feature was calculated for each frame; however, all values were averaged over the duration of the video clip (i.e., 25 frames) for their comparison with the imaging data.

Experimental Design, Task, and Procedure

The (f)MRI data used in this paper were collected as part of another study, with another study aim and analysis procedures. The original experiment consisted of two experimental sessions, one presenting face and voice stimuli and the other one body and voice stimuli. In each session, six experimental runs and an anatomical run were acquired. In addition, three different functional localizer runs were collected in total per subject. From this point onwards, only the stimuli, task and procedures concerning the current research goals will be described (i.e., body stimuli/runs). For a full description of the original study, see [Vaessen et al. \(2019\)](#).

The functional runs of the main experiment employed an event-related paradigm. Each run started with the presentation of the 16 video clips that comprised the body movement stimulus set, followed by 16 voice clips. Each trial started with a fixation cross, followed by the presentation of a 1-s clip, with an interstimulus interval of 10743–11246 ms (blank screen). In addition, each run presented four catch trials where participants had to indicate the change in the fixation cross color (i.e., red or blue) following the video. This was performed to ensure that participants were paying attention to the task while not explicitly directing their focus of attention to the explicit evaluation of the emotional expression. The total duration of each functional run was 8 min. For more details on stimuli presentation and functional localizer stimuli and design, see [Supplementary Materials](#).

(f)MRI Data Acquisition

Data were acquired with a 3 Tesla whole-body scanner (Siemens) located at the Maastricht Brain Imaging Centre (MBIC) of Maastricht University, the Netherlands. Functional images of the whole brain were obtained using T2*-weighted 2D echo-planar image (EPI) sequences (number of slices per volume = 50, 2 mm in-plane isotropic resolution, repetition time [TR] = 3000 ms, echo time [TE] = 30 ms, flip angle [FA] = 90°, field of view

[FoV] = 800 × 800 mm², matrix size = 100 × 100, multiband acceleration factor = 2, number of volumes per run = 160, total scan time per run = 8 min). The functional localizer scan also used a T2*-weighted 2D EPI sequence (number of slices per volume = 64, 2 mm in-plane isotropic resolution, TR = 2000 ms, TE = 31 ms, FA = 77, FoV = 800 × 800 mm², matrix size = 100 × 100, multiband acceleration factor = 2, number of volumes per run = 491, total scan time per run = 16 min approx.). Three-dimensional (3D) T1-weighted (MPRAGE GRAPPA2) imaging sequences were used to acquire high-resolution structural images for each participant (1-mm isotropic resolution, TR = 2250 ms, TE = 2.21 ms, FA = 9°, matrix size = 256 × 256, total scan time = 7 min approx.).

(f)MRI Data Preprocessing

BrainVoyager (v21.2 Brain Innovation B.V.) as well as custom code in MATLAB (vR2017a, The MathWorks Inc.) were used for the preprocessing and analysis of the acquired (f)MRI data. Trilinear/sinc estimation and interpolation were applied to correct for participant's 3D head motion with respect to the first volume of each functional run. Sinc interpolation was used to correct for time differences in slice acquisition order within one volume. High-pass temporal filtering was employed to exclude low-frequency drifts in the data lower than two cycles per run. The functional data of the main experiment were not spatially smoothed to preserve spatial specific information for the multivariate analyses. Spatial smoothing was applied, however, to the functional localizer data with a Gaussian kernel of a full-width half-maximum of 3 mm. The anatomical data were corrected for B1-field inhomogeneities. After these steps, the native functional and anatomical data were coregistered and template-based normalized to Talairach space ([Talairach and Tournoux 1988](#)).

Region of Interest Definition

The functional localizer data (see [Supplementary Materials](#)) were used to identify several regions of interest (ROI) for body perception. For this purpose, a fixed-effects whole-brain general linear model was fitted to the 3-mm-smoothed localizer data of each participant. The generated regression model consisted of the %-signal-transformed predictors of each stimulus category (i.e., body alone, face alone, voice alone 1, voice alone 2, body-voice, face-voice) convolved with a two-gamma hemodynamic

response function (HRF) and the z-transformed motion parameters as predictors of no interest.

The considered ROIs include: FBA, EBA, pSTS, V7/3a, superior parieto-occipital cortex (SPOC), superior marginal gyrus (SMG), posterior intraparietal sulcus (pIPS), medial intraparietal sulcus (mIPS), anterior intraparietal sulcus (aIPS), ventral and dorsal premotor cortex (PMv, PMd), SMA, pre-SMA, inferior frontal and frontal clusters. Body movement videos were contrasted to baseline at uncorrected $P=0.005$ to define the ROIs with the exception of FBA and EBA. For the latter, body movements were contrasted against facial movement clips at uncorrected $P=0.005$. The ROIs were defined bilaterally whenever possible and subsequently merged into a single ROI for each participant individually. For a detailed explanation of the definition and location of the ROIs, see [Supplementary Materials and Supplementary Table M1](#).

Representational Similarity Analysis

Representational similarity analyses (RSA) ([Kriegeskorte et al. 2008](#); [Nili et al. 2014](#)) were performed in MATLAB (vR2017a, The MathWorks Inc.) to investigate the relations among the computed features and brain activity. This type of analysis is based on the determination of representational dissimilarities between pairs of stimuli values. The representation is characterized by symmetrical matrices called representational dissimilarity matrices (RDMs). In these matrices, off-diagonal values reflect the dissimilarity between the values of two different stimuli while diagonal entries represent comparisons between identical stimuli and are zero by definition.

Computed-Feature RDMs

RDMs were constructed based on the dissimilarity between all stimulus pairs, in Euclidean distance, with respect to the computed feature values. Dummy variables were used to compute the emotional categories RDM, where the same emotion was defined as having zero dissimilarity with itself while two different emotions had a dissimilarity of $\sqrt{2}$. This analysis resulted in 16×16 distance matrices, one for each feature. To examine possible correlations among features, Spearman's rank correlations were performed.

Neural RDMs

In order to create neural RDMs for both the whole-brain searchlight and the ROI analyses, the β -values of each of the 16 body stimuli presented in the main experiment were used. These β -values were obtained after the application of an optimized HRF model to the data (see HRF estimation section in [Supplementary Materials](#)) ([Gardumi et al. 2016](#)). For each ROI, the β -values of each pair of stimuli were compared using Pearson's correlation r ($r=1$: perfect correlation; $r=-1$: perfect anticorrelation). Each possible stimulus-pair distance (d) was defined by $d=1-r$, where d ranges from 0 to 2. This generated a 16×16 distance matrix for each ROI and participant. In addition, every ROI dissimilarity matrix was correlated to each feature RDM using Spearman's rank correlation. The resulting correlation values were then z-transformed for each participant and a group-level one-sample t-test against 0 (two-tailed; Benjamini-Hochberg false discovery rate (BHFD)R-adjusted P -values) was computed for each feature.

A whole-brain searchlight (radius=5 voxels) analysis was performed using custom in-house MATLAB scripts. This approach allowed us to identify areas involved in the perception

of emotional body movements that were not covered by the defined ROIs. Similar to the ROI analyses, searchlight RDMs were correlated with each feature RDM using Spearman's rank correlation. The resulting maps were z-transformed for each participant. Subsequently, a group-level one-sample t-test against 0 (two-tailed, cluster size corrected with Monte-Carlo simulation, alpha level=0.05, initial $P=0.005$, numbers of iterations=5000) was computed for each feature. Univariate results are not reported in this paper, but see [Vaessen et al. \(2019\)](#) and [Supplementary Figure R3](#) in Supplementary Results.

Comparison Between Postural and Kinematic Feature Processing

Paired-sample t-tests were conducted to investigate whether the preselected ROIs processed kinematic and postural information differently. For each subject, we averaged the correlation values obtained for each feature-ROI comparison, separately for the postural features (i.e., shoulder ratio, surface, limb distances, symmetry, and limb angles), and kinematic ones (i.e., velocity, acceleration, and vertical movement). Subsequently, a paired-sample t-test was conducted per ROI comparing kinematic and postural values.

Comparison Between Dorsal and Ventral Processing of Body Features

We also investigated whether there was a difference in individual feature processing in dorsal and ventral clusters. For each subject, the correlation values obtained for each feature-ROI comparison were averaged within the dorsal (i.e., aIPS, mIPS, pIPS, V7/3a, SPOC, SMG, and pSTS) and ventral (i.e., EBA and FBA) ROIs. Next, a paired-sample t-test was conducted per feature.

Results

Kinematic and Postural Features

One of the aims of this study was the investigation of whether critical features of body posture and kinematics would reflect the emotional categorical structure of the body stimuli. These features were quantitatively computed from whole-body movement videos expressing an angry, fearful, happy, or an emotionally neutral expression (see [Fig. 1A](#)). To calculate the features, we estimated the location of the actors' main joints using the state-of-the-art 2D pose estimation library OpenPose (v1.0.1; [Cao et al. 2017](#)). Body features representing kinematic information comprised velocity, acceleration, and vertical movement. Postural features included limb angles, symmetry, shoulder ratio, surface, and limb contraction (for more information on feature definition, see [Table 1](#)). These features were selected for their demonstrated importance in previous literature (for a review, see [Kleinsmith and Bianchi-Berthouze 2012](#)).

Representational similarity analyses ([Kriegeskorte et al. 2008](#); [Nili et al. 2014](#)) were carried out to examine the relationship between emotion categories and the computed body features. This type of analysis is based on the estimation of the level of (dis)similarity between pairs of stimuli, which are characterized in the so-called RDMs (see Materials and Methods for more information on RDM computation). A first inspection of the RDMs revealed that kinematic body features (i.e., velocity, acceleration and vertical movement) do not clearly represent the categorical structure of emotion (see [Fig. 1B](#)). Generally, these features showed relatively high similarity between categories.

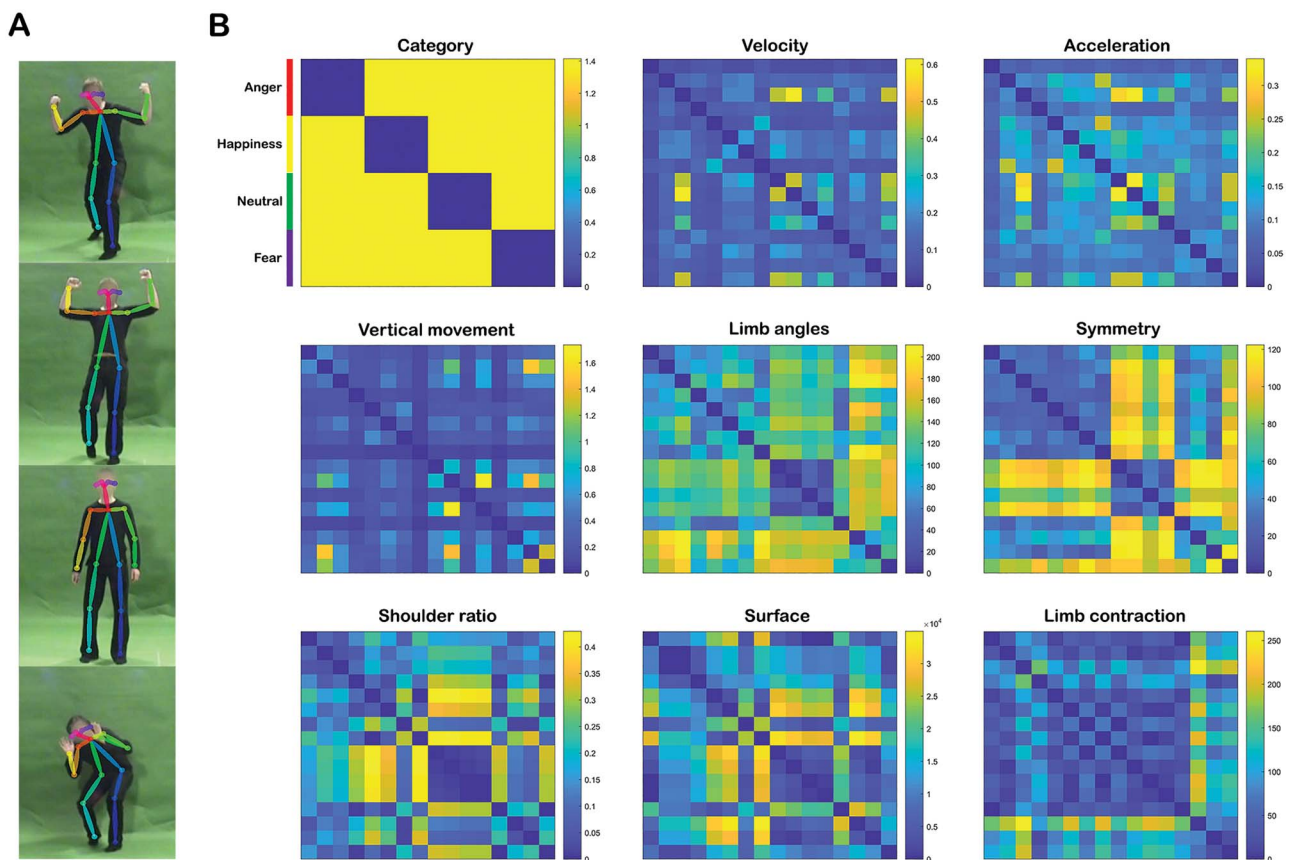


Figure 1. Representational dissimilarity matrices of the kinematic and postural features. (A) Examples of frames from the different affective movement videos with the OpenPose skeleton. Note that participants were shown the videos without the OpenPose skeleton; (B) The RDMs represent pairwise comparisons between the 16 stimuli with regard to the kinematic (i.e., velocity, acceleration, and vertical movement) and postural features (i.e., limb angles, symmetry, shoulder ratio, surface, and limb contraction) averaged over time. The dissimilarity measure reflects Euclidean distance, with blue indicating high similarity and yellow high dissimilarity. Color lines in the upper left corner indicate the organization of the RDMs with respect to the emotional category (anger: red; happiness: yellow; neutral: green; fear: purple) of the video stimuli.

Only velocity and acceleration showed a distinctive level of within-category similarity for the neutral condition. High within-category similarity was also found for neutral in the majority of postural features. In the case of symmetry, this finding was also accompanied by a high level of dissimilarity between neutral and the rest of the affective movement categories and a within- and between-category similarity for anger and happiness. The neutral and fearful conditions were different from the happy and angry categories for the features limb angles, shoulder ratio, and surface. Limb contraction was relevant for differentiating between fear and the rest of the categories.

Pairwise comparisons between kinematic and postural RDMs were performed to examine their interrelation and their relation to emotional categories (Fig. 2; see Supplementary Table R1 in Supplementary Results for correlation and P -values). This analysis was also conducted to further understand the results from the brain data (e.g., for understanding the nature of possible overlapping clusters resulting from different features or (dis)similarities in the pattern of feature representation between different ROIs). While kinematic features did not show significant correlations to emotion categories, postural features revealed weak to moderate significant correlations. Specifically, limb angles ($r(118)=0.408$, $p_{\text{Bonf}} < 0.001$), symmetry

($r(118)=0.349$, $p_{\text{Bonf}}=0.001$) and shoulder ratio ($r(118)=0.345$, $p_{\text{Bonf}}=0.001$) showed the strongest correlations to emotion. The relationship between postural and kinematic features was weak and often negative. Kinematic features correlated strongly among themselves, and similar findings were observed among postural features.

Kinematic and Postural Feature Representation in Predefined Areas

We also aimed at investigating whether the (dis)similarity of body posture and kinematics between different emotional categories could explain the neural response of brain regions involved in body processing. For this purpose, several areas were defined as ROI and their neural RDMs were computed and correlated to the emotional and feature RDMs. The ROIs included occipito-temporal areas that have previously shown a certain level of body specificity (three ROIs: FBA, EBA, and pSTS) (Downing et al. 2001; Peelen and Downing 2005; Schwarzlose et al. 2005; Kontaris et al. 2009; Vangeneugden et al. 2014), parietal and temporal areas thought to be implicated in attention and action observation (six ROIs: V7/3a, SPOC, SMG, PIPS, mIPS, and aIPS) (Culham and Valyear 2006; Grafton and Hamilton 2007; Corbetta et al. 2008; Caspers et al. 2010), and

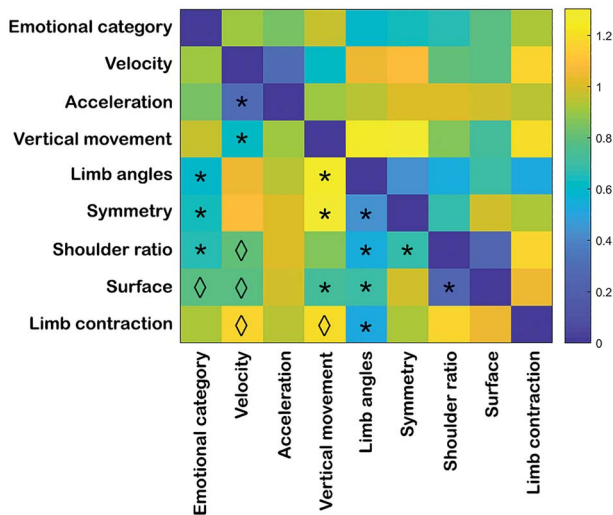


Figure 2. Correlation between RDMs of kinematic and postural features. The RDM represents the level of (dis)similarity between each of the kinematic (i.e., velocity, acceleration and vertical movement) and postural (i.e., limb angles, symmetry, shoulder ratio, surface, and limb contraction) matrices (see Fig. 1). Distances are indicated in 1-Spearman's correlation values, with blue indicating high similarity and yellow high dissimilarity. Asterisks and rhombi below the diagonal indicate significant correlations after Bonferroni correction and correlations that presented significant uncorrected P-values, respectively ($\alpha_{\text{bonf}} = 0.05/9$, with nine comparisons per feature; see [Supplementary Table R1](#) in Supplementary Results for correlation and P-values).

frontal areas involved in action observation and other higher cognitive functions (six ROIs: PMv, PMd, SMA, pre-SMA, inferior frontal, and frontal regions) ([Grafton and Hamilton 2007](#); [Caspers et al. 2010](#)). For more information regarding ROI definition and location, see Methods and Supplementary Materials. For an inspection of the ROI matrices, see [Supplementary Figure R1](#) in Supplementary Results.

The results showed that PMv (negatively, $r(10) = -0.03$, $p_{\text{uncorr.}} = 0.047$, $p_{\text{BHFD}} = 0.349$) and SMA (positively, $r(6) = 0.05$, $p_{\text{uncorr.}} = 0.004$, $p_{\text{BHFD}} = 0.066$) correlated significantly to emotion categories, but only before correction for multiple comparisons (see Fig. 3). The features representing kinematic features of body movement mainly displayed negative correlations to the majority of the defined ROIs. However, only the negative correlation between PMv and acceleration was significant before correction for multiple comparisons ($r(10) = -0.10$, $p_{\text{uncorr.}} = 0.031$, $p_{\text{BHFD}} = 0.397$). With regard to postural features, a significant positive correlation was found between pSTS and limb contraction ($r(11) = 0.10$, $p_{\text{BHFD}} = 0.038$). At uncorrected P-value, also between PMv and symmetry ($r(10) = 0.06$, $p_{\text{uncorr.}} = 0.043$, $p_{\text{BHFD}} = 0.689$), PMv and limb angles ($r(10) = 0.09$, $p_{\text{uncorr.}} = 0.044$, $p_{\text{BHFD}} = 0.441$), pre-SMA and surface ($r(4) = 0.10$, $p_{\text{uncorr.}} = 0.017$, $p_{\text{BHFD}} = 0.276$) and EVC and limb contraction ($r(12) = 0.11$, $p_{\text{uncorr.}} = 0.011$, $p_{\text{BHFD}} = 0.086$).

Next, paired-sample t-tests were performed to examine whether each individual ROIs processed kinematic and postural information differently. Only PMv showed a significant difference in the processing of kinematic ($M = -0.09$, $SD = 0.08$) and postural ($M = 0.04$, $SD = 0.05$) features at uncorrected P-value: $t(10) = -3.8$, $p_{\text{uncorr.}} = 0.004$, $p_{\text{Bonf}} = 0.056$ (see [Supplementary Table R2](#) in Supplementary Results for an overview of all paired-sampled t-tests). In addition, we investigated whether there was a difference in the processing of each individual feature with regard to dorsal (i.e., aIPS, mIPS,

PIPS, V7/3a, SPOC, SMG, and pSTS) and ventral (i.e., EBA and FBA) ROIs. Only velocity was processed significantly different in dorsal ($M = 0.03$, $SD = 0.15$) and ventral ROIs ($M = -0.06$, $SD = 0.15$) at uncorrected P-value: $t(12) = -2.23$, $p_{\text{uncorr.}} = 0.046$, $p_{\text{Bonf}} = 0.411$ (see [Supplementary Table R3](#) in Supplementary Results for an overview of all paired-sampled t-tests).

To investigate whether the defined ROIs contained unique affective body-movement representations, the group-averaged neural matrix of each ROI was correlated to that of the other ROIs. Overall, there was a relatively high similarity between and within parietal and temporo-occipital regions (see Fig. 4; see [Supplementary Table R4](#) in Supplementary Results for correlation and P-values). Specifically, SMG and EBA ($r(1538) = 0.64$, $p_{\text{Bonf}} < 0.001$), SMG and pSTS ($r(1538) = 0.58$, $p_{\text{Bonf}} < 0.001$), pIPS and EBA ($r(1538) = 0.57$, $p_{\text{Bonf}} < 0.001$), pSTS and EBA ($r(1538) = 0.57$, $p_{\text{Bonf}} < 0.001$) and pIPS and SMG ($r(1538) = 0.47$, $p_{\text{Bonf}} < 0.001$) showed the strongest significant positive correlations. The inferior frontal cluster and PMv also showed significant positive correlations with temporo-parietal areas. Although no significant negative correlations were found after Bonferroni correction, frontal and premotor regions presented some degree of dissimilarity, as well as frontal and ventral areas, and motor and parietal regions.

Whole-Brain Kinematic and Postural Feature Representation with Multivariate Approaches

In addition to body-selective regions, we also investigated whether (dis)similarities in body posture and kinematics between different emotional categories could explain the neural response at the whole-brain level. The computed feature RDMs were compared with the multivoxel dissimilarity fMRI patterns by means of searchlight RSA. The clusters resulting from this analysis are shown in [Supplementary Figure R2](#) and [Supplementary Table R5](#) in Supplementary Results. The velocity RDM was positively correlated to inferior frontal sulcus and precentral gyrus. Negative main effects for acceleration were found in middle temporal, superior frontal, and postcentral sulci while no positive main effects were observed for this feature. Vertical movement correlated positively with cingulate gyrus, whereas negatively to the frontomarginal and middle temporal gyri.

With respect to postural features, limb angles showed a positive main effect in anterior insula and pSTS. Several areas negatively correlated to symmetry in the inferior and middle occipital gyri, precuneus, isthmus, anterior calcarine, intraparietal, and cingulate sulci. Shoulder ratio negatively correlated to anterior insula, frontal operculum, putamen, ACC, middle frontal gyrus, cingulate sulcus, claustrum, internal capsule, and parahippocampal gyrus. Surface showed main negative effects in posterior orbital gyrus, thalamus, anterior perforated substance, ACC, inferior and superior frontal sulci, putamen, and internal capsule. Only positive correlations to limb contraction were found in intraparietal sulcus, anterior insula, caudate nucleus, amygdala, superior frontal sulcus and gyrus, precuneus, posterior orbital gyrus, ACC, superior temporal gyrus, inferior precentral sulcus, and SMG (see Fig. 5).

Whole-Brain Representation of Emotion

Our last research question was to investigate the representation of emotion at the whole-brain level. For this purpose, a searchlight RSA was computed with the emotion category

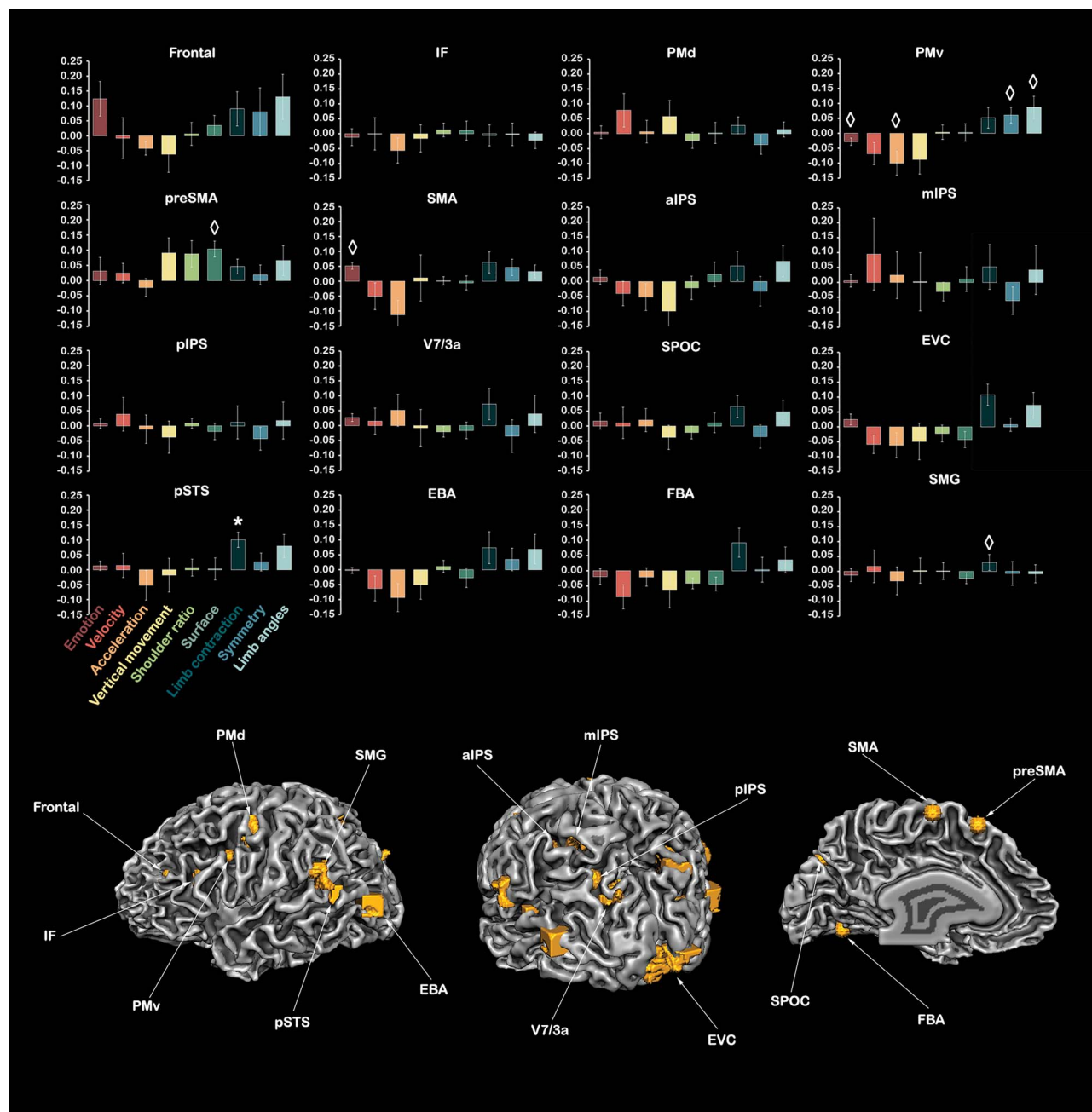


Figure 3. Average Spearman's rank correlation across participants between the kinematic/postural feature RDMs and each ROI matrix. Kinematic features include velocity, acceleration, and vertical movement. Postural features comprise shoulder ratio, surface, limb contraction, symmetry, and limb angles. Positive r values indicate that a high (dis)similarity between a stimulus pair in the feature RDM also has a high (dis)similarity in the neural representation. A negative correlation means that a low (dis)similarity between two stimuli at the feature level would have a higher (dis)similarity in the neural representation. Asterisks and rhombi indicate significant correlations after BHFDR correction and correlations that presented significant uncorrected P -values, respectively (one sample t -test against 0, two-tailed). The error bars denote the standard error of the mean (SEM). Order or relationships across ROIs are not assumed here. Abbreviations: EBA, extrastriate body area; EVC, early visual cortex; FBA, fusiform body area; IF, inferior frontal cortex; IPS, intraparietal sulcus; p, posterior; m, middle; a, anterior; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; pre-SMA, presupplementary motor area; pSTS, posterior superior temporal sulcus; SMA, supplementary motor area; SMG, supramarginal gyrus; SPOC, superior parietal occipital cortex.

RDM. This analysis showed that no area presented a main effect of emotion after correction for multiple comparisons. Before correction, however, several regions correlated positively to emotion, including inferior temporal cortex, anterior insula, lingual sulcus, superior frontal gyrus, and lateral occipital sulcus

(see [Supplementary Table R6](#) in Supplementary Results for an overview of the clusters showing a main effect of emotion at uncorrected P -value). Interestingly, negative main effects of emotion were found in amygdala, inferior frontal, and middle temporal gyri.

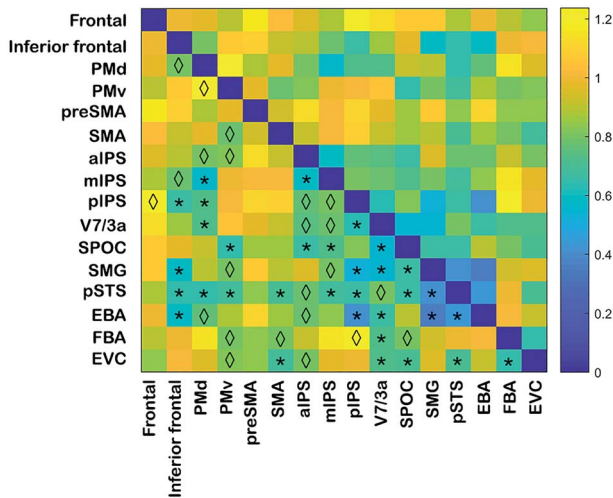


Figure 4. Correlation between ROI RDMs. For each ROI, a group-averaged RDM was obtained. Subsequently, pairwise comparisons between the resulting group ROI matrices were performed. The dissimilarity measure reflects 1-Spearman's rank correlation values, with blue indicating strong similarity and yellow strong dissimilarity. Rhombi and asterisks below the diagonal indicate significant correlations before and after Bonferroni correction for multiple comparisons, respectively ($\alpha_{\text{Bonf}} = 0.05/16$, with 16 comparisons per ROI, see Supplementary Results, [Supplementary Table R4](#)). Abbreviations: EBA, extrastriate body area; EVC, early visual cortex; FBA, fusiform body area; IPS, intraparietal sulcus; p, posterior; m, middle; a, anterior; PMd, dorsal premotor cortex; PMv, ventral premotor cortex; pre-SMA, presupplementary motor area; pSTS, posterior superior temporal sulcus; SMA, supplementary motor area; SMG, supramarginal gyrus; SPOC, superior parietal occipital cortex.

Discussion

The present study investigated the mechanisms underlying body expression perception by measuring the brain representation of critical features of body movement and posture. Our results reveal six major findings. First, computationally defined features are systematically related to distributed brain areas. Second, postural rather than kinematic features reflect the affective category structure of the body movements. Limb angles and symmetry were important for differentiating neutral from emotional body movements. Limb angles and especially limb contraction were particularly relevant for distinguishing fear from other body expressions. These two features were represented in several regions including affective, action observation and motor preparation networks. Third, the pSTS differentiated fearful from other affective categories using limb contraction rather than kinematics, despite this area being known for its involvement in biological motion processing. Fourth, EBA and FBA also showed greater tuning to postural features. Although the pattern of feature representation in these areas was similar, the stimuli representation in EBA was very dissimilar to that of FBA, possibly reflecting their different roles in body processing. Fifth, kinematic and postural feature processing was not segregated into dorsal and ventral streams, with the exception of one feature: velocity. Finally, the brain representation of emotional categories showed a distributed pattern. In the sections below, we elaborate on our findings in more detail and propose the reasons why our quantitative description of naturalistic whole-body movements moves the field forward.

Relationship Between Emotion Concepts and Subsymbolic Body Features

Our findings revealed differential effects of posture and movement features. Postural features allowed clearer distinctions between different emotional categories (see [Fig. 1](#)), while kinematic features showed high similarity across emotions (see [Fig. 1](#)) and weak correlations with emotional categories (see [Fig. 2](#)). The importance of postural features was already postulated as an ethologically important property by Darwin ([Darwin 1872](#); [Hinde and Rowell 1962](#)), being indicative of socio-affective displays of submission and dominance in conspecific individuals. This pattern is also consistent with previous research showing the importance of postural information for affect recognition (for a review, see [Kleinsmith and Bianchi-Berthouze 2012](#)). For example, [Atkinson et al. \(2007\)](#) reported that while motion cues may be sufficient for emotional recognition, the disruption of form information disproportionately compromises the recognition performance, especially in the case of fear. The present results are also in agreement with those found in a behavioral study with a larger stimulus set that included the current 16 video clips ([Poyo Solanas et al. 2020](#)), indicating that our stimulus set is representative of a larger set.

The majority of postural features clearly distinguished emotional from nonemotional body movements, such as limb angles, shoulder ratio, and surface. This was clearest in the symmetry RDM, possibly because emotional movements are less symmetrical than nonemotional ones ([Poyo Solanas et al. 2020](#)). Limb angles, shoulder ratio, and surface also showed dissimilarities in the representation of happy and anger from fear and neutral expressions. This might be due to the degree of openness of the body, bigger for angry and happy expressions, and lower neutral and fearful ones (for a review, see [Kleinsmith and Bianchi-Berthouze 2012](#)). In line with previous work, the degree of limb contraction seems to be relevant for distinguishing fear from other affective movements ([Roether et al. 2009](#); [Poyo Solanas et al. 2020](#)).

While we chose to average feature information over time, the use of another calculation approach could have benefited the representation of the kinematics of each video. We considered as an alternative using the maximum kinematic value per video. However, this may not have been representative of the entire video and therefore, may have resulted in a poor or misleading correspondence to participants' activity patterns. Also, this approach may have not been comparable between postural and kinematic features. A next step in understanding body expression perception is the study of these features in relation to brain activity.

Limb Contraction and Fear Perception

The stimuli representation of limb contraction showed a clear distinction between fear and other affective movements ([Roether et al. 2009](#); [Poyo Solanas et al. 2020](#)). This feature positively correlated to cortical and subcortical areas spanning affective perception, action observation, and motor preparation and execution networks. Interestingly, these areas are also known for their involvement in body expression processing, especially fearful ones ([de Gelder 2006](#); [Meeren et al. 2016](#)). At the subcortical level, there was a high amount of overlap between areas correlating to limb contraction and to the postural features of shoulder ratio and surface (see [Fig. 5](#) and [Supplementary Table R5](#) in Supplementary Results). However,

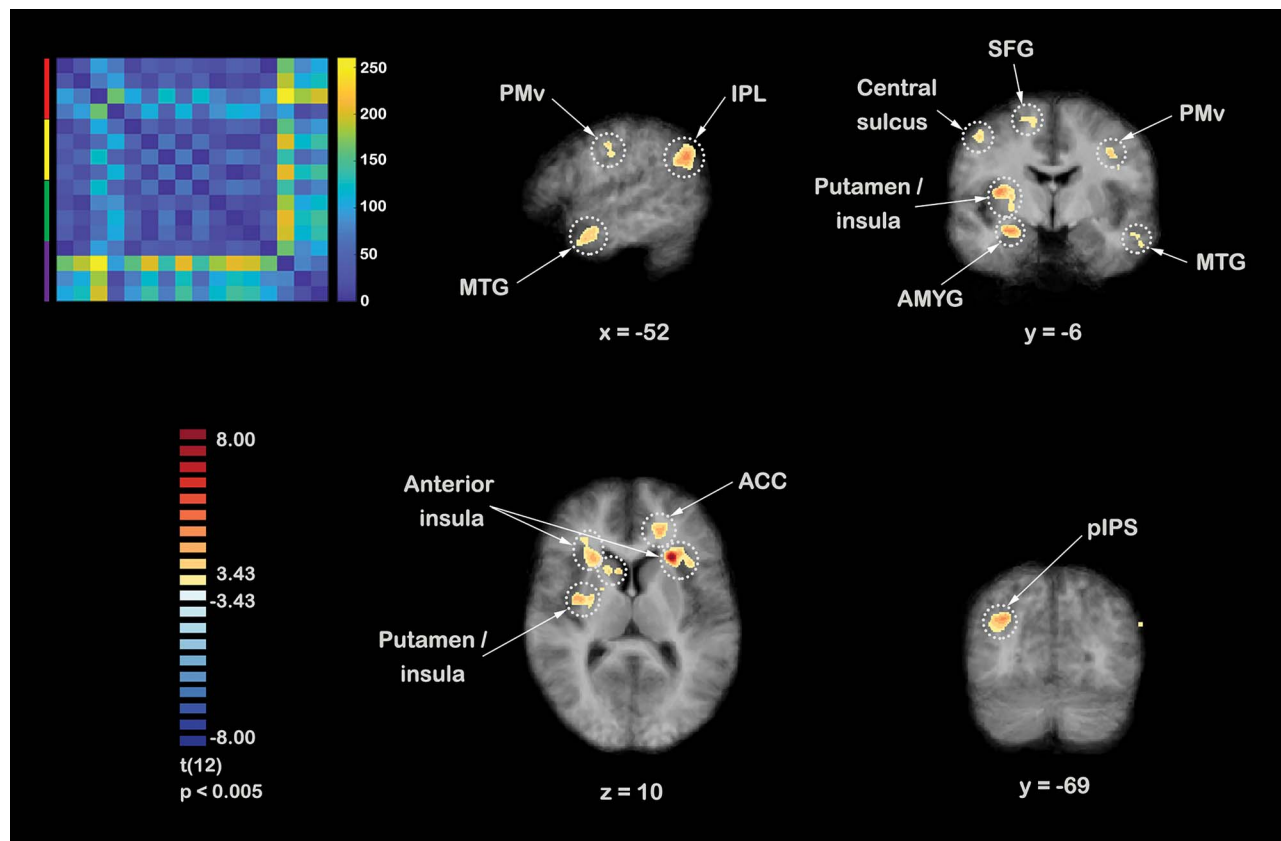


Figure 5. Clusters resulting from the searchlight RSA of the postural feature of limb contraction. The multivoxel fMRI dissimilarity matrices were correlated to the limb contraction RDM (upper left corner). The limb contraction RDM represents pairwise comparisons between the 16 stimuli with regard to limb contraction information averaged over time. The dissimilarity measure reflects Euclidean distance, with blue indicating high similarity and yellow high dissimilarity. Color lines indicate the organization of the RDM with respect to the emotional category (anger: red; happiness: yellow; neutral: green; fear: purple) of the video stimuli. Spearman's rank correlation was used to correlate the limb contraction RDM to the multivoxel fMRI dissimilarity matrices. The resulting maps were z-transformed for each participant. Subsequently, a group-level one-sample t-test against 0 was performed (two-tailed, cluster size corrected with Monte-Carlo simulation, alpha level = 0.05, initial $P = 0.005$, numbers of iterations = 5000). See [Supplementary Table R5](#) in Supplementary Results for more details on location and statistical values of the clusters. Abbreviations: ACC, anterior cingulate cortex; AMYG, amygdala; IPL, inferior parietal lobule; MTG, middle temporal gyrus; pIPS, posterior intraparietal sulcus; PMv, ventral premotor cortex; SFG, superior frontal gyrus.

limb contraction was the only feature positively correlated to these areas. Also, the stimuli representation of this feature was dissimilar to those of shoulder ratio and surface (see [Fig. 2](#) and [Supplementary Table R1](#) in Supplementary Results). Taken together, these findings suggest that the stimuli representation in these overlapping clusters was more similar to the representation reflected by limb contraction.

One of these areas is the caudate nucleus, a subcortical region that has been implicated in the automatic and rapid perception of emotional bodies ([de Gelder 2006](#)) as well as in goal-directed behaviors, by integrating information related to motor behavior, actions and space ([Grahn et al. 2008](#)). In particular, the caudate nucleus may influence motor planning due to its connections with motor cortices ([Utter and Basso 2008](#)) and structures that have been implicated in the affective evaluation of the environment, such as the insula ([Chikama et al. 1997](#); [Craig 2009](#)) and the amygdala ([Emery and Amaral 2000](#)). Interestingly, these areas were also positively correlated to limb contraction. Another subcortical area known for being involved in motor planning and execution, the putamen ([Grahn et al. 2008](#)), also correlated positively to limb contraction. Cortical areas also part of the action observation network and thought to be involved

in motor preparation were observed, including pIPS, PMv, pre-SMA, and IPL. In particular, pIPS has been implicated in attention and action observation ([Culham and Valyear 2006](#); [Grafton and Hamilton 2007](#); [Corbetta et al. 2008](#); [Caspers et al. 2010](#)) while PMv and pre-SMA have been involved in space perception, action, and intention understanding ([Rizzolatti et al. 1996, 2002](#); [Lau et al. 2004](#); [Urgesi, Calvo-Merino, et al. 2007a](#); [Urgesi, Candidi, et al. 2007b](#)), as well as in action preparation and execution ([Luppino et al. 1991](#); [Picard and Strick 2001](#); [Isoda 2005](#); [Hoshi and Tanji 2007](#)). Interestingly, a recent TMS study has directly implicated the IPL in the recognition of fearful body expressions ([Engelen et al. 2015](#)).

Limb contraction was also significantly related to areas known to be implicated in emotional regulation and body awareness. One of these areas is the insula, a cortical region that has been suggested to integrate information about the location and condition of our bodies, our subjective emotions and the key features of our environment. Thus, this area may be a key player in associating internal and external experiences ([Critchley 2005](#); [Karnath et al. 2005](#); [Craig 2009](#)). Other areas also thought to play a role in monitoring the internal emotional state as well as in attention selection and planning, correlated

positively to limb contraction, including the ACC (Devinsky et al. 1995), the orbitofrontal cortex (Beer et al. 2006), and the dorsolateral prefrontal cortex (Phillips et al. 2003). The amygdala also showed a positive correlation to limb contraction. For decades, this area has been suggested to have a central role in the rapid perception and response to fear (LeDoux 2003), and its relation to fearful body expressions has already been established (Hadjikhani and de Gelder 2003). Through its connections to sensory cortical regions, this area is thought to modulate attentional and perceptual processes and tune the motor system to initiate adaptive behaviors (Emery and Amaral 2000). Interestingly, the amygdala has shown to present connections to many of the brain regions correlating to limb contraction (Emery and Amaral 2000).

In sum, the present results indicate that the processing of limb contraction may be a crucial link in understanding how body expressions automatically trigger fear perception. Previous electromyography studies have associated muscle activity to specific whole-body expressions (Huis In 't Veld et al. 2014a, 2014b). When experiencing fear, the associated muscle contractions give rise to a contracted body posture by flexion of the limbs (Huis In 't Veld et al. 2014a). Although the defined features in this study reflect spatial displacement rather than muscle activity, the feature limb contraction can be seen as a clear representation of fear-related muscle contractions. Taken together, these findings make the limb contraction feature a logical candidate for triggering fear perception processes. Ultimately, the distinctive fear contraction posture, the underlying muscle activity and the literature on freezing behavior (Roelofs 2017) converge here to underscore the importance of these results in the broader framework of affective neuroscience.

The Brain Representation of Limb Angles

Limb angles showed positive correlations to several areas that have previously been implicated in the processing of emotions: precentral gyrus, anterior insula, superior temporal sulcus, and postcentral gyrus (Kober et al. 2008; Dricu and Frühholz 2016). These regions have been suggested to play a role in action observation and motor preparation (i.e., precentral and postcentral gyrus) (Grafton and Hamilton 2007; Caspers et al. 2010; Valchev et al. 2016), interoception (i.e., anterior insula) (Critchley 2005; Karnath et al. 2005; Craig 2009) and biological motion processing (i.e., superior temporal sulcus) (Allison et al. 2000; Grossman et al. 2000; Grossman et al. 2010). Their similarity to the stimuli representation of limb angles indicates that these areas may be relevant in the distinction between neutral and emotional categories, as well as between fearful and other body expressions (see Fig. 1).

The Representation of Kinematic and Postural Features in Body Category Areas

Previous studies on the brain basis of whole-body expressions have reported systematic relations between emotion categories and the activity of areas known for body category representation, albeit the emphasis has often been on a network of areas larger than these body specific areas (de Gelder 2006). Three areas in the occipito-temporal cortex have previously shown body-category selectivity: FBA, EBA, and pSTS (Downing et al. 2001; Peelen and Downing 2005; Schwarzlose et al. 2005; Kontaris et al. 2009; Vangeneugden et al. 2014). EBA and FBA are hypothesized to be involved in body form processing, while pSTS

is thought to be involved in body motion processing (Peelen et al. 2006; Grossman et al. 2010; Grosbras et al. 2012). However, the role of these body-selective areas in expression perception is still a matter of debate (Downing and Peelen 2011). Our findings on body feature representation contribute to clarify the role of these body-selective areas in body expression perception.

It appears from our results that EBA and FBA do not represent kinematic aspects of affective movements but show greater sensitivity to postural cues, although not consistently or reaching significance (see Fig. 3). Previous proposals based on studies of neutral still body images attributed body-part representation to EBA while the processing of whole-bodies to FBA (Taylor et al. 2007; Urgesi, Calvo-Merino, et al. 2007a; Hodzic et al. 2009). This functional division does not clearly reflect a corresponding specialization for parts versus whole processing for expression recognition in EBA and FBA. The majority of studies have involved these two body-selective areas in expression processing (Peelen and Downing 2007) with as yet no clear proposal for a division of labor. Our results contribute important new information by showing that body expression representation in EBA was dissimilar to that of FBA (see Fig. 4 and Supplementary Table R4 in Supplementary Results), although the pattern of feature representation was similar in these areas (see Fig. 3). Overall, these findings suggest different roles in body processing for EBA and FBA. This clear difference may at least be partially related to the different anatomical connections of EBA and FBA (Zimmermann et al. 2018) and also to their internal heterogeneity (Weiner and Grill-Spector 2011). Consistent with the pattern of anatomical connectivity of EBA and its specific internal complexity, we found that SMG, pSTS, pIPS, and the inferior frontal cortex represent body movements in a similar manner to EBA but dissimilar from FBA (see Fig. 4 and Supplementary Table R4 in Supplementary Results). The observed neural similarity between these areas and EBA in affective body processing fits with the fact that these areas are known areas for playing a role in action perception and preparation (de Gelder 2006; Goldberg et al. 2014) and that EBA is strongly connected to parietal cortex regions (Zimmermann et al. 2018).

A third area involved in body processing and more specifically in expression perception is pSTS (Wegrzyn et al. 2015; Zhang et al. 2016; Basil et al. 2017). A surprising result is that we did not find a representation of kinematic body features in pSTS despite previous studies involving this area in the processing of biological motion (Allison et al. 2000; Grossman et al. 2000; Grossman et al. 2010). For example, the multivariate analysis showed that pSTS processed differently movements that had similar vertical displacement of the body joints, and regardless of the emotion conveyed (see Fig. 5 and Supplementary Table R5 in Supplementary Results). Against this negative finding in view of the literature, we do find a novel contribution of pSTS as our ROI analyses specifically revealed that fearful body movements might be represented differently from other affective categories in this area. Furthermore, our analyses showed that pSTS may use the information conveyed by the contraction of the limbs to perform this discrimination (see Figs 1 and 3). Specifically, body movements with similar limb contraction characteristics were processed similarly in pSTS (see Fig. 3). This result is in line with previous studies showing the involvement of this area in the recognition of emotions (Wegrzyn et al. 2015; Zhang et al. 2016; Basil et al. 2017), especially when the expression conveyed depicts fear (Grèzes et al. 2007; Candidi et al. 2011). Further research will be needed to clarify how pSTS codes for emotion and to understand how and which features this area uses and

in combination with which other areas for the discrimination between affective body movements.

The Representation of Kinematic and Postural Features Outside Body-Category Areas

Besides the well-known body-category areas, other body-selective regions were defined that are also involved in action observation and other higher cognitive functions (see Results and Materials and Methods). One of these areas is pre-SMA. This area showed a positive correlation to the feature of surface (see Fig. 3), which discriminated neutral and fearful expressions from happy and angry ones (see Fig. 1). Pre-SMA may use this body feature to understand the intention behind the observed movement (Lau et al. 2004) and prepare for an appropriate motor response (Luppino et al. 1991; Isoda 2005).

Among all the predefined ROIs, PMv stands out for processing kinematic and postural features differently, being more tuned to postural information (see Results and Supplementary Table R2 in Supplementary Results). This area processed body movements with comparable symmetry and limb-angle values in a similar manner, irrespective of acceleration (see Fig. 3 and Supplementary Table R2 in Supplementary Results). This finding contrasts with previous TMS studies involving this area in the processing of actions regardless of body posture (Urgesi, Candidi, et al. 2007b; Candidi et al. 2011). Here, the stimuli representation of these features suggests that PMv processed neutral and fearful body movements differently from the rest of the emotion categories (see Fig. 1), in agreement with previous neuroimaging (Pichon et al. 2008; Kret et al. 2011b; Calbi et al. 2017) and TMS studies (Balconi and Bortolotti 2013; Engelen et al. 2018). Interestingly, PMv has also been involved in action preparation and execution (Picard and Strick 2001; Hoshi and Tanji 2007) as well as in space perception and action understanding (Rizzolatti et al. 1996, 2002; Urgesi, Calvo-Merino, et al. 2007a; Urgesi, Candidi, et al. 2007b). Taken together, these results suggest PMv as the convergence point between perception and motor processes, possibly contributing to the elaboration of an appropriate response when encountering a threatening body, based on coding this feature.

Differences in Kinematic and Postural Feature Processing in Dorsal and Ventral Streams

According to the classical view of visual processing (Vaina et al. 1990; Giese and Poggio 2003; Milner and Goodale, 2006, 2008), form and movement information are processed in two separate pathways in the brain. However, in the current study, the only kinematic feature that was represented differently in dorsal (i.e., aIPS, mIPS, pIPS, V7/3a, SPOC, SMG, and pSTS) and ventral (i.e., EBA and FBA) areas was velocity (see Results and Supplementary Table R3 in Supplementary Results). Particularly, dorsal regions processed body movements with comparable velocity characteristics in a similar manner and regardless of the conveyed affect, whereas ventral areas represented body movements differently despite presenting similar velocity values. This is in line with the view that the dorsal stream is specialized in processing motion signals irrespective of visual forms while ventral areas use structural information rather than kinematic cues to differentiate between stimuli (Vaina et al. 1990; Giese and Poggio 2003; Milner and Goodale, 2006, 2008). However, no clear dorsal versus ventral stream segregation was observed for the

rest of the features, challenging the classical two-stream model of visual processing.

Distributed Representation of Emotional Expressions in the Brain

We performed RSA in predefined regions (i.e., ROI RSA) and at the whole-brain level (i.e., whole-brain searchlight RSA) to investigate the symbolic representation of emotion. Overall, our results clearly show that a number of different areas are involved in whole-body expression perception by processing visual body features. In the predefined ROIs, the only significant positive correlation with emotion was found in SMA (see Fig. 3), an area that has been related to action representation and motor preparation (Nachev et al. 2008), and thought to be strongly impacted by emotion expression (Oliveri et al. 2003; Rodigari and Oliveri 2014; Engelen et al. 2018). Based on its connections to the amygdala (Grèzes et al. 2014), it has been proposed that SMA may play a role in transforming affective experience into motor actions (Oliveri et al. 2003). Our multivariate analyses showed that SMA may discriminate between emotional body movements using limb contraction information and thus, this area may be important in the discrimination of fearful body expressions (see Fig. 1).

Whole-brain RSA revealed that the emotional content conveyed by body movements (i.e., emotion RDM) is coded in middle temporal and occipital areas (see Fig. 5 and Supplementary Table R5 in Supplementary Results). The location of these areas differed from the ones of the predefined clusters. The region located in the middle temporal gyrus has been suggested to play a role in movement observation (Rizzolatti et al. 1996) as well as in the attribution of intentions to others (Brunet et al. 2000).

Limitations, Perspectives, and Future Work

Comparable methodological approaches to the one employed here have been previously used to investigate body processing in the brain. For instance, RSA has been used to elucidate the organizational principles of body part representations (Bracci et al. 2015). Multivariate methods have also been employed to investigate subcategorical processing of bodies. For example, Orlov and colleagues (2014) showed that the kinematic profiles of the upper limbs can be decoded from upper-limb-selective OTC regions and the hMT+ (Orlov et al. 2014). Wurm and Lingnau (2015) recently revealed the underlying brain mechanisms of action understanding at different levels of abstraction (Wurm and Lingnau 2015). However, the focus of these approaches in affective neuroscience has mostly been on body parts and affective whole-body expressions rather than on midlevel body features. Our study was motivated by the need to develop a more detailed theory of whole-body expression representation in the brain, aiming at understanding the underlying mechanisms better than has so far been achieved by high-level symbolic theories of visual perception and emotion.

Furthermore, research on subsymbolic feature representation in affective signal processing may build a bridge between animal and human research, as we try to understand how relatively simple stimulus features (e.g., postural features) rather than high-level information (i.e., fully processed whole-body images) can already trigger perception and prepare for adaptive action, two basic skills we expect a biological system to be equipped with. While complex emotions (e.g., fear) in daily life

are often associated with rich stimuli (i.e., a fully recognized intimidating whole-body expression), a fraction of that information may be sufficient for the brain to reach an interpretation about ongoing events and prepare for adaptive action. Studies on face and body perception with EEG and MEG have found evidence for the processing of the emotional significance of a stimulus in a time window around 80–100 ms (Pizzagalli et al. 2002; Van Heijnsbergen et al. 2007; Meeren et al. 2016). Our findings suggest that this early activity may be related to the presence of features rather than to the high-level processing of whole faces or bodies, and that this information may be sufficient for the brain to conclude the presence of a threat and initiate action preparation processes.

By investigating midlevel feature processes, this study moves the field of affective neuroscience forward, providing insights into the perceptual features that possibly drive automatic emotion perception. Features at this visual computational level may only partly overlap with feature descriptions used in everyday descriptions of body expressions (Poyo Solanas et al. 2020). Nevertheless, it is important to be aware of the limitations of our findings. For instance, the features defined here were selected due to their relevance in the literature because no feature-based and biologically plausible computational model of naturalistic body expressions is available (Giese and Poggio 2003; Serre 2014). We expect that future studies will also use larger and more diverse stimulus sets with a wider range of affective states and a larger participant sample.

Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

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Competing Interests

The authors declare no competing interests.

References

- Allison T, Puce A, McCarthy G. 2000. Social perception from visual cues: role of the STS region. *Trends Cogn Sci*. 4:267–278.
- Atkinson AP, Tunstall ML, Dittrich WH. 2007. Evidence for distinct contributions of form and motion information to the recognition of emotions from body gestures. *Cognition*. 104:59–72.
- Balconi M, Bortolotti A. 2013. The “simulation” of the facial expression of emotions in case of short and long stimulus duration. The effect of pre-motor cortex inhibition by rTMS. *Brain Cogn*. 83:114–120.
- Basil RA, Westwater ML, Wiener M, Thompson JC. 2017. A causal role of the right superior temporal sulcus in emotion recognition from biological motion. *Open Mind*. 2:26–36.
- Beer JS, John OP, Scabini D, Knight RT. 2006. Orbitofrontal cortex and social behavior: integrating self-monitoring and emotion-cognition interactions. *J Cogn Neurosci*. 18:871–879.
- Bracci S, Caramazza A, Peelen MV. 2015. Representational similarity of body parts in human occipitotemporal cortex. *J Neurosci*. 35:12977–12985.
- Brunet E, Sarfati Y, Hardy-Baylé MC, Decety J. 2000. A PET investigation of the attribution of intentions with a nonverbal task. *Neuroimage*. 11:157–166.
- Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ. 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci*. 13:400–404.
- Calbi M, Angelini M, Gallese V, Umiltà MA. 2017. “Embodied body language”: an electrical neuroimaging study with emotional faces and bodies. *Sci Rep*. 7:6875.
- Candidi M, Stienen BM, Aglioti SM, de Gelder B. 2011. Event-related repetitive transcranial magnetic stimulation of posterior superior temporal sulcus improves the detection of threatening postural changes in human bodies. *J Neurosci*. 31:17547–17554.
- Cao Z, Simon T, Wei S-E, Sheikh Y. 2017. Realtime multi-person 2d pose estimation using part affinity fields. *Proc IEEE Comput Soc Conf Comput Vis Pattern Recognit*. 7291–7299.
- Caspers S, Zilles K, Laird AR, Eickhoff SB. 2010. ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*. 50:1148–1167.
- Chikama M, McFarland NR, Amaral DG, Haber SN. 1997. Insular cortical projections to functional regions of the striatum correlate with cortical cytoarchitectonic organization in the primate. *J Neurosci*. 17:9686–9705.
- Corbetta M, Patel G, Shulman GL. 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron*. 58:306–324.
- Coulson M. 2004. Attributing emotion to static body postures: recognition accuracy, confusions, and viewpoint dependence. *J Nonverbal Behav*. 28:117–139.
- Craig AD. 2009. How do you feel—now? The anterior insula and human awareness. *Nat Rev Neurosci*. 10:59–70.
- Critchley HD. 2005. Neural mechanisms of autonomic, affective, and cognitive integration. *J Comp Neurol*. 493:154–166.
- Culham JC, Valyear KF. 2006. Human parietal cortex in action. *Curr Opin Neurobiol*. 16:205–212.
- Darwin C. 1872. *The expression of emotions in animals and man*. London (UK): Murray.
- de Gelder B. 2006. Towards the neurobiology of emotional body language. *Nat Rev Neurosci*. 7:242.
- de Gelder B, Snyder J, Greve D, Gerard G, Hadjikhani N. 2004. Fear fosters flight: a mechanism for fear contagion when perceiving emotion expressed by a whole body. *PNAS*. 101:16701–16706.
- De Meijer M. 1989. The contribution of general features of body movement to the attribution of emotions. *J Nonverbal Behav*. 13:247–268.
- Decety J, Grèzes J, Costes N, Perani D, Jeannerod M, Procyk E, Grassi F, Fazio F. 1997. Brain activity during observation of actions. Influence of action content and subject’s strategy. *Brain*. 120:1763–1777.
- Devinsky O, Morrell MJ, Vogt BA. 1995. Contributions of anterior cingulate cortex to behaviour. *Brain*. 118:279–306.
- Downing PE, Jiang Y, Shuman M, Kanwisher N. 2001. A cortical area selective for visual processing of the human body. *Science*. 293:2470–2473.
- Downing PE, Peelen MV. 2011. How might occipitotemporal body-selective regions interact with other brain areas to support person perception? *Cogn Neurosci*. 2:216–226.

- Dricu M, Fröhholz S. 2016. Perceiving emotional expressions in others: activation likelihood estimation meta-analyses of explicit evaluation, passive perception and incidental perception of emotions. *Neurosci Biobehav Rev.* 71: 810–828.
- Emery NJ, Amaral DG. 2000. The role of the amygdala in primate social cognition. In: Land R, Nadel L, editors. *Cognitive neuroscience of emotion*. New York: Oxford University Press, pp. 156–191.
- Engelen T, de Graaf TA, Sack AT, de Gelder B. 2015. A causal role for inferior parietal lobule in emotion body perception. *Cortex.* 73:195–202.
- Engelen T, Zhan M, Sack AT, de Gelder B. 2018. Dynamic interactions between emotion perception, action perception, and action preparation areas for reacting to social threat: a combined cTBS-fMRI study. *eNeuro.* 5:ENEURO-0408-17.2018.
- Fogassi L, Ferrari PF, Gesierich B, Rozzi S, Chersi F, Rizzolatti G. 2005. Parietal lobe: from action organization to intention understanding. *Science.* 308:662–667.
- Gardumi A, Ivanov D, Hausfeld L, Valente G, Formisano E, Uludağ K. 2016. The effect of spatial resolution on decoding accuracy in fMRI multivariate pattern analysis. *Neuroimage.* 132:32–42.
- Giese MA, Poggio T. 2003. Neural mechanisms for the recognition of biological movements. *Nat Rev Neurosci.* 4:179–192.
- Giese MA, Rizzolatti G. 2015. Neural and computational mechanisms of action processing: interaction between visual and motor representations. *Neuron.* 88:167–180.
- Goldberg H, Preminger S, Malach R. 2014. The emotion–action link? Naturalistic emotional stimuli preferentially activate the human dorsal visual stream. *Neuroimage.* 84:254–264.
- Grafton ST, Arbib MA, Fadiga L, Rizzolatti G. 1996. Localization of grasp representations in humans by positron emission tomography. *Exp Brain Res.* 112:103–111.
- Grafton ST, Hamilton AF. 2007. Evidence for a distributed hierarchy of action representation in the brain. *Hum Mov Sci.* 26:590–616.
- Grahn JA, Parkinson JA, Owen AM. 2008. The cognitive functions of the caudate nucleus. *Prog Neurobiol.* 86:141–155.
- Grèzes J, Pichon S, de Gelder B. 2007. Perceiving fear in dynamic body expressions. *Neuroimage.* 35:959–967.
- Grèzes J, Valabrègue R, Gholipour B, Chevallier C. 2014. A direct amygdala-motor pathway for emotional displays to influence action: a diffusion tensor imaging study. *Hum Brain Mapp.* 35:5974–5983.
- Grosbras MH, Beaton S, Eickhoff SB. 2012. Brain regions involved in human movement perception: a quantitative voxel-based meta-analysis. *Hum Brain Mapp.* 33:431–454.
- Grossman E, Donnelly M, Price R, Pickens D, Morgan V, Neighbor G, Blake R. 2000. Brain areas involved in perception of biological motion. *J Cogn Neurosci.* 12:711–720.
- Grossman E, Jardine N, Pyles J. 2010. fMR-adaptation reveals invariant coding of biological motion on human STS. *Front Hum Neurosci.* 4:15.
- Hadjikhani N, de Gelder B. 2003. Seeing fearful body expressions activates the fusiform cortex and amygdala. *Curr Biol.* 13:2201–2205.
- Hinde RA, Rowell TE. 1962. Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proc Zool Soc.* 138:1–21.
- Hodzic A, Kaas A, Muckli L, Stirn A, Singer W. 2009. Distinct cortical networks for the detection and identification of human body. *Neuroimage.* 45:1264–1271.
- Hoshi E, Tanji J. 2007. Distinctions between dorsal and ventral premotor areas: anatomical connectivity and functional properties. *Curr Opin Neurobiol.* 17:234–242.
- Huis In 't Veld EMJ, van Boxtel GJM, de Gelder B. 2014a. The body action coding system I: muscle activations during the perception and expression of emotion. *Soc Neurosci.* 9: 249–264.
- Huis In 't Veld EMJ, van Boxtel GJM, de Gelder B. 2014b. The body action coding system II: muscle activations during the perception and expression of emotion. *Front Behav Neurosci.* 8:330.
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G. 2005. Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol.* 3:e79.
- Isoda M. 2005. Context-dependent stimulation effects on saccade initiation in the presupplementary motor area of the monkey. *J Neurophysiol.* 93:3016–3022.
- Jellema T, Baker C, Wicker B, Perrett D. 2000. Neural representation for the perception of the intentionality of actions. *Brain Cogn.* 44:280–302.
- Johansson G. 1973. Visual perception of biological motion and a model for its analysis. *Percept Psychophys.* 14:201–211.
- Karnath H-O, Baier B, Nägele T. 2005. Awareness of the functioning of one's own limbs mediated by the insular cortex? *J Neurosci.* 25:7134–7138.
- Kirby LA, Robinson JL. 2017. Affective mapping: an activation likelihood estimation (ALE) meta-analysis. *Brain Cogn.* 118:137–148.
- Kleinsmith A, Bianchi-Berthouze N. 2012. Affective body expression perception and recognition: a survey. *IEEE T Affect Comput.* 4:15–33.
- Kober H, Barrett LF, Joseph J, Bliss-Moreau E, Lindquist K, Wager TD. 2008. Functional grouping and cortical-subcortical interactions in emotion: a meta-analysis of neuroimaging studies. *Neuroimage.* 42:998–1031.
- Kontaris I, Wiggett AJ, Downing PE. 2009. Dissociation of extrastriate body and biological-motion selective areas by manipulation of visual-motor congruency. *Neuropsychologia.* 47:3118–3124.
- Kret M, Pichon S, Grèzes J, de Gelder B. 2011a. Men fear other men most: gender specific brain activations in perceiving threat from dynamic faces and bodies—an fMRI study. *Front Psychol.* 2:3.
- Kret M, Pichon S, Grèzes J, de Gelder B. 2011b. Similarities and differences in perceiving threat from dynamic faces and bodies. An fMRI study. *Neuroimage.* 54:1755–1762.
- Kriegeskorte N, Mur M, Ruff DA, Kiani R, Bodurka J, Esteky H, Tanaka K, Bandettini PA. 2008. Matching categorical object representations in inferior temporal cortex of man and monkey. *Neuron.* 60:1126–1141.
- Lau HC, Rogers RD, Haggard P, Passingham RE. 2004. Attention to intention. *Science.* 303:1208–1210.
- LeDoux J. 2003. The emotional brain, fear, and the amygdala. *Cell Mol Neurobiol.* 23:727–738.
- Lindquist KA, Wager TD, Kober H, Bliss-Moreau E, Barrett LF. 2012. The brain basis of emotion: a meta-analytic review. *Behav Brain Sci.* 35:121.
- Luppino G, Matelli M, Camarda R, Gallese V, Rizzolatti G. 1991. Multiple representations of body movements in mesial area 6 and the adjacent cingulate cortex: an intracortical microstimulation study in the macaque monkey. *J Comp Neurol.* 311:463–482.

- Meeren HK, Hadjikhani N, Ahlfors SP, Hämäläinen MS, De Gelder B. 2016. Early preferential responses to fear stimuli in human right dorsal visual stream—a MEG study. *Sci Rep.* 6: 24831.
- Milner D, Goodale MA. 2006. *The visual brain in action*. Oxford (UK): Oxford University Press.
- Milner D, Goodale MA. 2008. Two visual systems re-viewed. *Neuropsychologia.* 46:774–785.
- Nachev P, Kennard C, Husain M. 2008. Functional role of the supplementary and pre-supplementary motor areas. *Nat Rev Neurosci.* 9:856–869.
- Nili H, Wingfield C, Walther A, Su L, Marslen-Wilson W, Kriegeskorte N. 2014. A toolbox for representational similarity analysis. *PLoS Comput Biol.* 10:e1003553.
- Oliveri M, Babiloni C, Filippi MM, Caltagirone C, Babiloni F, Cicinelli P, Traversa R, Palmieri MG, Rossini PM. 2003. Influence of the supplementary motor area on primary motor cortex excitability during movements triggered by neutral or emotionally unpleasant visual cues. *Exp Brain Res.* 149:214–221.
- Orlov T, Porat Y, Makin TR, Zohary E. 2014. Hands in motion: an upper-limb-selective area in the occipitotemporal cortex shows sensitivity to viewed hand kinematics. *J Neurosci.* 34:4882–4895.
- Paterson HM, Pollick FE, Sanford AJ. The role of velocity in affect discrimination. *Proceedings of the Annual Meeting of the Cognitive Science Society*; 2001.
- Patwardhan A. 2017. Three-dimensional, kinematic, human Behavioral pattern-based features for multimodal emotion recognition. *Multimodal Technol Interact.* 1:19.
- Peelen MV, Downing PE. 2005. Selectivity for the human body in the fusiform gyrus. *J Neurophysiol.* 93:603–608.
- Peelen MV, Downing PE. 2007. The neural basis of visual body perception. *Nat Rev Neurosci.* 8:636.
- Peelen MV, Wiggett AJ, Downing PE. 2006. Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. *Neuron.* 49:815–822.
- Phillips ML, Drevets WC, Rauch SL, Lane R. 2003. Neurobiology of emotion perception I: the neural basis of normal emotion perception. *Biol Psychiatry.* 54:504–514.
- Piana S, Stagliano A, Odone F, Verri A, Camurri A. 2014. Real-time automatic emotion recognition from body gestures. arXiv preprint arXiv:1402.5047.
- Picard N, Strick PL. 2001. Imaging the premotor areas. *Curr Opin Neurobiol.* 11:663–672.
- Pichon S, de Gelder B, Grèzes J. 2008. Emotional modulation of visual and motor areas by dynamic body expressions of anger. *Soc Neurosci.* 3:199–212.
- Pichon S, de Gelder B, Grèzes J. 2009. Two different faces of threat. Comparing the neural systems for recognizing fear and anger in dynamic body expressions. *Neuroimage.* 47:1873–1883.
- Pizzagalli DA, Lehmann D, Hendrick AM, Regard M, Pascual-Marqui RD, Davidson RJ. 2002. Affective judgments of faces modulate early activity (~160 ms) within the fusiform gyri. *Neuroimage.* 16:663–677.
- Pollick FE, Paterson HM, Bruderlin A, Sanford AJ. 2001. Perceiving affect from arm movement. *Cognition.* 82:B51–B61.
- Poyo Solanas M, Vaessen M, de Gelder B. 2020. The role of computational and subjective features in emotional body expressions. *Sci Rep.* 10:1–13.
- Rizzolatti G, Fadiga L, Gallese V, Fogassi L. 1996. Premotor cortex and the recognition of motor actions. *Cogn Brain Res.* 3:131–141.
- Rizzolatti G, Fogassi L, Gallese V. 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. *Nat Rev Neurosci.* 2:661.
- Rizzolatti G, Fogassi L, Gallese V. 2002. Motor and cognitive functions of the ventral premotor cortex. *Curr Opin Neurobiol.* 12:149–154.
- Rodrigari A, Oliveri M. 2014. Disrupting SMA activity modulates explicit and implicit emotional responses: an rTMS study. *Neurosci Lett.* 579:30–34.
- Roelofs K. 2017. Freeze for action: neurobiological mechanisms in animal and human freezing. *Philos T R Soc B.* 372:20160206.
- Roether CL, Omlor L, Christensen A, Giese MA. 2009. Critical features for the perception of emotion from gait. *J Vis.* 9:15–15.
- Sawada M, Suda K, Ishii M. 2003. Expression of emotions in dance: relation between arm movement characteristics and emotion. *Percept Mot Skills.* 97:697–708.
- Schwarzlose RF, Baker CI, Kanwisher N. 2005. Separate face and body selectivity on the fusiform gyrus. *J Neurosci.* 25:11055–11059.
- Serre T. 2014. Hierarchical models of the visual system. In: Jung R, Jaeger D, editors. *Encyclopedia of computational neuroscience*. New York: Springer.
- Talairach J, Tournoux P. 1988. *Co-planar stereotaxic atlas of the human brain: 3d proportional system: an approach to cerebral imaging*. New York: Georg Thieme Verlag.
- Taylor JC, Wiggett AJ, Downing PE. 2007. Functional MRI analysis of body and body part representations in the extrastriate and fusiform body areas. *J Neurophysiol.* 98:1626–1633.
- Urgesi C, Calvo-Merino B, Haggard P, Aglioti SM. 2007a. Transcranial magnetic stimulation reveals two cortical pathways for visual body processing. *J Neurosci.* 27:8023–8030.
- Urgesi C, Candidi M, Ionta S, Aglioti SM. 2007b. Representation of body identity and body actions in extrastriate body area and ventral premotor cortex. *Nat Neurosci.* 10:30.
- Utter AA, Basso MA. 2008. The basal ganglia: an overview of circuits and function. *Neurosci Biobehav Rev.* 32:333–342.
- Vaessen M, Abassi E, Mancini M, Camurri A, de Gelder B. 2018. Computational feature analysis of body movements reveals hierarchical brain organization. *Cereb Cortex.* 1:10.
- Vaessen M, Van der Heijden K, de Gelder B. 2019. Decoding of emotion expression in the face, body and voice reveals sensory modality specific representations. *bioRxiv.* 869578.
- Vaina LM, Lemay M, Bienfang DC, Choi AY, Nakayama K. 1990. Intact “biological motion” and “structure from motion” perception in a patient with impaired motion mechanisms: a case study. *Vis Neurosci.* 5:353–369.
- Valchev N, Gazzola V, Avenanti A, Keysers C. 2016. Primary somatosensory contribution to action observation brain activity—combining fMRI and cTBS. *Soc Cogn Affect Neurosci.* 11:1205–1217.
- Van den Stock J, Tamietto M, Sorger B, Pichon S, Grèzes J, de Gelder B. 2011. Cortico-subcortical visual, somatosensory, and motor activations for perceiving dynamic whole-body emotional expressions with and without striate cortex (V1). *PNAS.* 108:16188–16193.
- Van Heijnsbergen C, Meeren H, Grèzes J, de Gelder B. 2007. Rapid detection of fear in body expressions, an ERP study. *Brain Res.* 1186:233–241.
- Vangeneugden J, Peelen MV, Tadin D, Battelli L. 2014. Distinct neural mechanisms for body form and body motion discriminations. *J Neurosci.* 34:574–585.
- Wallbott HG. 1998. Bodily expression of emotion. *Eur J Soc Psychol.* 28:879–896.

- Wegrzyn M, Riehle M, Labudda K, Woermann F, Baumgartner F, Pollmann S, Bien CG, Kissler J. 2015. Investigating the brain basis of facial expression perception using multi-voxel pattern analysis. *Cortex*. 69:131–140.
- Weiner KS, Grill-Spector K. 2011. Not one extrastriate body area: using anatomical landmarks, hMT+, and visual field maps to parcellate limb-selective activations in human lateral occipitotemporal cortex. *Neuroimage*. 56:2183–2199.
- Wurm MF, Lingnau A. 2015. Decoding actions at different levels of abstraction. *J Neurosci*. 35:7727–7735.
- Zhang H, Japee S, Nolan R, Chu C, Liu N, Ungerleider LG. 2016. Face-selective regions differ in their ability to classify facial expressions. *Neuroimage*. 130:77–90.
- Zimmermann M, Mars RB, De Lange FP, Toni I, Verhagen L. 2018. Is the extrastriate body area part of the dorsal visuomotor stream? *Brain Struct Funct*. 223:31–46.