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ORIGINAL ARTICLE

Computational Feature Analysis of Body Movements Reveals Hierarchical Brain Organization

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Abstract

Social species spend considerable time observing the body movements of others to understand their actions, predict their emotions, watch their games, or enjoy their dance movements. Given the important information obtained from body movements, we still know surprisingly little about the details of brain mechanisms underlying movement perception. In this fMRI study, we investigated the relations between movement features obtained from automated computational analyses of video clips and the corresponding brain activity. Our results show that low-level computational features map to specific brain areas related to early visual- and motion-sensitive regions, while mid-level computational features are related to dynamic aspects of posture encoded in occipital–temporal cortex, posterior superior temporal sulcus and superior parietal lobe. Furthermore, behavioral features obtained from subjective ratings correlated with activity in higher action observation regions. Our computational feature-based analysis suggests that the neural mechanism of movement encoding is organized in the brain not so much by semantic categories than by feature statistics of the body movements.

Key words: body, computational analysis, fMRI, movement

Introduction

Social species spend considerable time observing the body movements of others, whether it is to understand their actions, predict their emotions, watch their success at games, or enjoy their expansive dance movements. Given the importance of the information obtained from watching body movements, we still know surprisingly little about the neural mechanisms. Body movements convey a broad range of information such as action, intention, emotion, and esthetic qualities and have so far been individually addressed. Furthermore, very few studies in the literature have gone beyond the use of semantic and qualitative categories to look into how the brain represents underlying movement features.

Research on action observation has shown that the human frontoparietal mirror network plays a role in detecting and processing actions and intentions (Rizzolatti and Craighero 2004; Urgesi et al. 2007). Another domain of body research has investigated how bodies convey affective information (de Gelder et al. 2004; de Gelder 2006, 2016; Grezes et al. 2007; Goldberg et al. 2015; Meeren et al. 2016). Current findings have shown close links between emotion perception and (pre-) motor structures (Borgomaneri et al. 2015; Engelen et al. 2015; de Gelder 2016), interactions between ventral and dorsal areas (Zimmermann et al. 2017), and cross talk between the amygdala, pulvinar and motor and prefrontal structures (Pessoa and Adolphs 2010;

Tamietto and de Gelder 2010). Studies on the neural correlates of dance movements have investigated the role of the motor component in dance observation. Some of these were directly motivated by the concept of mirror neurons and the role of dance expertise in watching dance (Calvo-Merino et al. 2006), while others studied the esthetic dimension (Kirsch et al. 2013) and addressed qualitative questions about the esthetic experience triggered in the observer (Calvo-Merino et al. 2008; Cross et al. 2011) associated with watching dance performances.

Another domain of body-related research focuses on “embodiment,” a process that is traditionally referred to as “putting oneself in the skin of the other” or empathy in its original meaning of perspective taking (Ruby and Decety 2001; Thirioux et al. 2009). It relates to the observers’ ability of projecting oneself onto another body or mentally inhabiting an observed body. Indeed, Blanke (2012) found a neural basis specific for illusory self-identification i.e., experiencing another body as one’s own. The brain’s ability for external embodiment may also play a role in understanding whole-body movements.

Almost all the studies mentioned so far have focused on localizing the neural correlates of selected movement categories that were defined semantically. There are currently very few examples of analytical and quantitative approaches to movement perception that look into the neural correlates of detailed movement features rather than at such broad semantic categories. One exception are studies of features of movement kinematics. McAleer et al. showed that body part speed and distance of the body parts to each other were related to brain activity in extrastriate and posterior superior temporal cortex (McAleer et al. 2014). Casile and collaborators (Casile et al. 2010) compared the levels of blood oxygen level-dependent activity elicited by human actions that either complied with or violated kinematic laws. The former only activated left dorsal premotor, dorsolateral prefrontal cortex, and medial frontal cortex. Another recent study that gets closer to understanding movement features and brain activity calculated the relation between the motion index (an index of whole-body movement) and brain activation (Noble et al. 2014). Results showed that the motion index was related to brain activity in a single cluster in the right inferior temporal gyrus, an area frequently reported in the studies of body movement perception as seen in a recent meta-analysis (Grosbras et al. 2012).

To summarize, with the exception of studies on the neural correlates of movement kinematics, body movements have so far been studied in a holistic way and by using a qualitative approach, with the research questions guided by semantics of object category (faces, bodies, houses, etc.) and type of information (identity, emotion, etc.). A major obstacle for understanding the underlying mechanisms so far has been the lack of an analytical model of movement perception (Giese and Poggio 2003). Thus, for a better understanding of the underlying brain mechanisms, it seems that focusing on features of human body movement is crucial. Analogous to classical hierarchical feature models of visual object recognition (Tanaka 1997), a viable hypothesis is that the brain processes whole-body movements by coding a range of movement features at different levels of complexity and ultimately arrives at a coherent percept through feature integration. As an example in line with this, recent monkey studies found that information in the mid-superior temporal sulcus (STS) related to body category perception is organized in the brain not so much by semantic categories than by feature statistics of the body (Popivanov et al. 2016). Yet, there is currently no example of a hierarchical computational model-based approach to visual processes involved in movement perception in humans.

Investigating the neural mechanisms of movements in dance perception offers some clear advantages. Researchers have found that dance images are increasingly deemed appropriate to study how the brain processes perception of whole-body movement (Calvo-Merino et al. 2006; Blasing et al. 2012). Dance movements are relatively abstract in the sense that they are not directly designed for nor produced to convey familiar

Table 1 Description of cFeatures and bFeatures

Features based on computational model (cFeatures)	
cAcceleration (low level)	Acceleration of the sensor along the three (x,y,z) axes. Basic measurement of the IMU
cMagneticOrientation (low level)	The orientation of the sensor with respect to the earth magnetic field. Basic measurement of the IMU
cGyro (low level)	Angular acceleration. Basic measurement of the IMU
cEnergy (low level)	Kinetic energy (KE) averaged over wrist sensors
cPeriodicity (mid level)	Periodicity is an index that tends to one if the input energy varies in a periodical (repetitive, with a fixed period) way, it tends to zero otherwise (nonregular/repetitive variation). The FFT of the average KE is computed and the harmonics exhibiting the first and second strongest magnitudes are extracted. Periodicity depends on the difference in magnitude between these two harmonics (i.e., we consider more periodic a signal exhibiting a great difference in magnitude between the first and second harmonic)
cSymmetry (mid level)	Dynamic symmetry as a mid-level feature by considering the coordination and dynamics of parts of the body. We compute the difference of jerk and energy between the right and left hands. Then we take the minimum between the two differences as the value of symmetry
cLightness (mid level)	Lightness is computed from the average of the magnitude of the vertical component of KE of the two wrists IMU’s of the dancer normalized by the whole-body vertical component of KE of wrists and ankles IMU’s. See Niewiadomski et al. (2017) for details
Features based on behavioral rating (bFeatures)	
bMotion	The degree of movement displayed
bSymmetry	The degree of symmetry displayed by the body
bEnergy	The degree of energy in the movement
bSmoothness	The degree of fluency displayed by the movement
bGravity	The degree of downward movement/direction displayed
bBalance	The degree of balance displayed by the movement
bTension	The degree of clenching

semantic information such as common action intentions or emotions. Therefore, pragmatic or cognitive interpretations associated with more complex processes are not automatically triggered as, for example, in the case of familiar actions. Even when whole-body movements found in a dance context still carry semantics that trigger interpretations that are abstracted and all the more so when the fragments are short and disconnected. In the present study, we investigated the neural mechanisms of movement perception guided by a detailed computational model. This hierarchical model distinguishes low, mid level, and higher order features (Camurri et al. 2016). Conceptually, this model is inspired by the classical movements analysis of Laban (Groff 1995).

Our experimental conditions consisted of two familiar characteristics of body movements: "lightness and fragility," two labels commonly used to describe qualities of movement and inspired by Labanian movement analysis theory (Groff 1995) (see Supplementary Material, for details). For the sake of clarity we refer to these as *eLighness and eFragility*. The specific motivation for choosing lightness and fragility was that they are features in the computational model of dance that we use (Camurri et al. 2016). (They are computed by the algorithms processing the sensor data). When referring to these as computational features rather than as semantic categories or experimental conditions, we use the term *cFeatures*. Furthermore, in this computational model, the features are organized hierarchically in the sense that some features are considered low-level measurement features, as they are obtained from the accelerometer sensors directly after basic filtering, whereas others are considered mid-level features that are computed from the low-level features, see Niewiadomski et al. (2017) and Table 1. Importantly, this hierarchical model allows us to look separately at low and mid-level features and compare this activity at different levels of the brain's processing hierarchy.

Our main hypotheses concerned the relation between algorithmic features from the computer model (*cFeatures*) and brain activation obtained from fMRI scans and our predictions are about the relation between these different features. We expect that cFeatures taken from either the low- or the mid-level computer model hierarchy would map to brain areas at different levels of the visual processing hierarchy. Furthermore, in a separate behavioral study, we obtained subjective ratings of a number of movement characteristics for each video (behavioral or *bFeatures*). This allowed us to ask whether the cFeatures also have a systematic relation with the ratings obtained for the bFeatures. The relation between brain activity and the features was analyzed using representational similarity analysis (RSA) (Nili et al. 2014).

Methods

Participants

Twelve healthy participants (mean age = 24.8 years; age range = 22–35 years; 10 female; two left-handed participants) were recruited. Inclusion criteria were normal or corrected-to-normal vision, a medical history without any psychiatric or neurologic disorders as well as no previous (semi)professional dance training and no interest in frequently attending dance performances. Participants were recruited following the guidelines of the ethical committee at Maastricht University and were informed about the task and the general safety rules of (f)MRI scanning and remained unaware of the aim of the study. During fMRI scanning naïve participants (without dance experience either as amateur performers or observers) passively viewed examples of the two semantic movement categories consisting of approximately 10-s video clips. Written consent was obtained from all participants. The experiment was carried out in accordance with the Declaration of Helsinki. Participants either received credit points or were reimbursed with monetary reward after their participation in the scan session.

A separate large sample of participants was tasked with the behavioral rating of the stimuli. Forty-eight physically and neurologically healthy participants (36 females and 12 males) were recruited for this online survey (age $M = 23$ years, range = 19–44 years). Participants were dance naïve or had limited dance experience. Due to the high number of stimuli ($n = 120$) and to prevent participant fatigue, stimuli were divided equally among five questionnaires (sets 24 stimuli each). Stimuli were presented in a randomized order to limit an order effect and each participant watched each video clip only once. Participants were asked to assign each video to one of the two conditions (fragility or lightness) and to rate its movement features on a number of Likert scales related to (see Table 1 for details).

Stimuli and Experimental Design

Ten female semiprofessional dancers were individually instructed by a professional choreographer to perform movements in the two types of semantic dance categories: lightness and fragility (Camurri et al. 2016; Niewiadomski et al. 2017) and were recorded on video. All dancers were wearing black clothes, had hair tied in a black cap, and were fitted with accelerometers (inertial measurement unit, IMU, x-OSC sensors: http://x-io.co.uk/x-osc) on the wrists, ankles, and waist, see Supplementary Figure 1. During dance performances, continuous data from these devices were recorded at 50 Hz and low-pass prefiltered with a cutoff frequency of 2 Hz. In a later stage, the kinematic computational features were calculated from these data, using either all or a subset of the sensors available (see Table 1 for details). The videos were edited into six approximately 10-s fragments for each dancer and dance type, resulting in 120 videos. The faces were blurred to avoid face-related processing by the fMRI participants. For an example of a dancer performing Fragile movements, see https://youtu.be/XcEhc0_uuvA.

In the fMRI scanner, participants passively watched (while free viewing) the videos presented in a randomized order with a 12 (±2)-s interval between each video. To reduce fatigue, the experiment was split into three runs of approximately 15 min.

MRI Data Acquisition

The MRI data were acquired at the Maastricht Brain Imaging Center, Maastricht University (the Netherlands), with a 3 T MAGNETOM Prisma fit scanner (Siemens), with a 64-channel head–neck receiver coil. We acquired two anatomical scans, including a T1-weighted image (3D MPRAGE, FOV = 224 mm, matrix = 320 × 320, 256 sagittal slices in a single slab, TR = 2400 ms, TE = 2.14 ms, TI = 1000 ms, GRAPPA = 2) and a T2-weighted image (SPACE, same matrix, FOV, and slices as in the T1w, TR = 3200 ms, TE = 565 ms, GRAPPA = 2). Functional images were acquired with a T2*-weighted gradient echo EPI sequence, covering the whole brain with a resolution of 2 × 2 × 2 mm (64 slices without gaps, TR = 1330 ms, TE = 30 ms, multiband acceleration factor = 3, FOV = 200 × 200, matrix size = 100 × 100, phase encoding direction: anterior to posterior). To correct for EPI distortion, an extra run of five volumes with phase encoding direction posterior to anterior was acquired before each functional run.

Image Analysis

A specialized high-quality preprocessing pipeline from the Human Connectome Project (HCP, https://www.humanconnectome.org/ (Glasser et al. 2013)) was used to preprocess the fMRI data. This pipeline consists of a set of state-of-the-art tools to allow accurate comparison of brain anatomy and functional activation across subjects as well as noise reduction. Briefly, the anatomical images were aligned to a standard space (MNI) template through a series of optimized automatic processes. This included bias field removal by computing a bias field from a combination of the T1- and T2-weighted images. During this process, the brain is also segmented into the main tissue types and a 3D model of the cortical surface is generated to allow an even more accurate comparison of cortical areas among subjects. Here, the T2-weighted image is used to fine-tune the gray matter/pial boundary. The functional images are first corrected for MRI sequence-induced anatomical distortions (Andersson and Sotiropoulos 2015), further corrected for between image head motion, coregistered to the anatomical and MNI space images, and finally spatially smoothed with a 2-mm FWMH Gaussian kernel. These fMRI images were then used to perform the statistical analyses.

We applied several different analysis methods to the data: voxel-based GLM contrasts, multivoxel classification, and multivoxel searchlight RSA. Each of these approaches has its own objectives and merits. The GLM analysis is useful in mapping regions activated by the stimuli and revealing where a stimulus category elicits higher activation. However, single voxels' contrasts are not sensitive to regional multivoxel patterns, which is why we included multivoxel methods to 1) map brain regions where the two experimental conditions, fragility and lightness, could be classified and 2) reveal parts of the brain where there is a correspondence between the movement features and brain patterns.

Activation Mapping and Contrasting

We used a general linear model approach to test for differences in voxel-level brain activations between the two dance conditions. At the single-subject level, a fixed-effects whole-brain general linear model analysis was performed in the MNI-normalized functional images. For this purpose, a regression model was generated consisting of the predictors for each of the two conditions. The motion predictors and their first derivatives were included into the model as nuisance predictors. At the group level, a random-effects general linear model was performed to investigate the contrasts of Lightness>Fragility and Fragility>Lightness. The GLM analyses were performed with SPM12 software (http://www.fil.ion.ucl.ac.uk/spm/software/spm12).

Gaussian Naïve Bayes Decoder

A multivoxel decoder based on a Gaussian naïve Bayes (GNB) classifier was performed at the single-subject level, using custom in-house MATLAB scripts (Ontivero-Ortega et al. 2017). First, a new fixed-effects GLM model with predictors for the 3 runs and 40 stimuli per run was fitted to the minimally smoothed data to obtain beta values for each stimulus presentation. Next, a whole-brain searchlight (radius = 5 voxels) approach was used to map regions of the cortex where the regional multivoxel beta values from the GLM contained decodable information on the two dance conditions. To obtain groupwise information on classification accuracies, the single-subject accuracy maps were centered at 50% accuracy and entered in a second-level *t*-test.

RSA Analyses

The GLM model with 120 stimuli from the GNB analysis was also used for the RSA analysis using in-house MATLAB scripts. In the first-level (stimulus-level) analysis, a neural representational dissimilarity matrix (RDM) was constructed by calculating for all stimulus pairs a distance value $d(i,j)$ between stimuli i and j, where $d = 1 - r$. The value r is Pearson's correlation coefficient between the multivoxel beta values of the local searchlight neighborhood for the pair of stimuli i and j. This produced RDMs of 120 × 120 elements for each voxel in the searchlight mask. To examine the relation between the neural RDM and putative stimulus models, several reference matrices were constructed: from the semantic categories fragility and lightness (zero dissimilarity within conditions, positive equal dissimilarity between conditions); from the actor identity (zero dissimilarity within actor, positive equal dissimilarity between actors); and from the computational features derived from the accelerometers and the feature ratings obtained from the participants (see Table 1). The dissimilarity for a pair of stimuli for the cFeature RDMs was defined by $d = 1 - r$, where r is Pearson's correlation coefficient between the histogram bins for the cFeature values of the two stimuli. The dissimilarity for a pair of stimuli for the bFeatures RDMs were defined by d, where d is the Euclidean distance between the Likert scale rating for the two stimuli. For the second-level analyses, statistical inferences were performed after transforming these correlation values into Fisher's Z values. Neural and model RDMs were compared using Spearman rank correlation.

In a second analysis, the different model RDMs were combined in a single regression model to assess the combined contribution of the RDMs to the neural multivoxel patterns. Model RDMs were first elementwise squared (Carlin and Kriegeskorte 2017) and the *t*-statistics for the beta coefficient, accounting for the shared variance between RDMs, were tested at the group level as in the previous RSA analyses.

Group-level analyses were performed on the surface after mapping volume-space, single-subject values (*t*-maps for the GLM, accuracies for GNB, and searchlight maps for RSA) to their individual surface maps. Next, all analyses were done using the FSL PALM tool with permutation testing, $n = 500$ permutations with Gamma approximation enabled (this option runs a small number of permutations and computes empirically the moments of the permutation distribution, then fits a gamma distribution for the final inference). Spatial statistics where computed by the TFCE algorithm based on the statistical maps from the permutation step. Contrasts were investigated at $P < 0.05$ TFCE FWE correction (Winkler et al. 2014).

Results

Differences in Activation and Patterns Between the Stimulus Conditions

We first investigated the functional brain activation of the stimuli and the univariate voxelwise differences in brain activation between the two stimulus conditions with an RFX-GLM. Compared with baseline (crosshair fixation), the stimuli, as expected, activated the visual cortex, occipitotemporal cortex (OTC), STS, inferior parietal lobule (IPL), superior parietal lobule (SPL), and fusiform cortex (see Fig. 1A). Then the two experimental conditions were compared with each other. eLightness showed higher activations in occipital pole, cuneus, and intracalcarine cortex ($P < 0.05$ TFCE FWE) (see Fig. 1B). eFragility did not show any significant higher activation compared to eLightness.

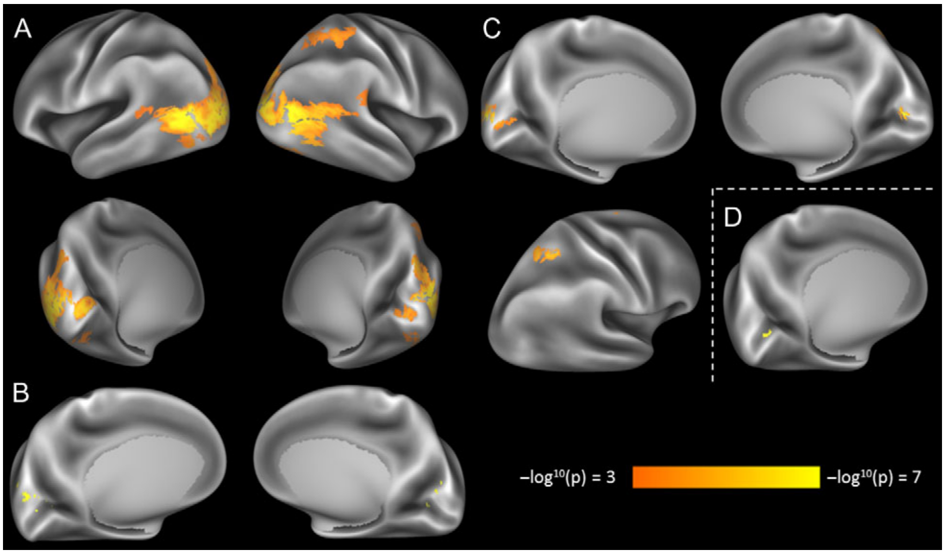

Figure 1. (*A*) Results of the group-level GLM for the contrast of stimulus viewing versus baseline (crosshair). (*B*) Results of the second-level GLM for the contrast Lightness>Fragility. (*C*) Results of the second-level GNB classifier. (*D*) Results of the second-level RSA on semantic categories (Fragility and Lightness). Yellow colors indicate log transformed *P*-values of the respective statistical tests (thresholded at $P < 0.05$ TFCE FWE). Color bar refers to panel A.

Second, we assessed whether a searchlight GNB classifier could decode multivoxel patterns separating the two dance conditions. This analysis revealed multivoxel patterns containing information discriminating between the two conditions in the left occipital pole, middle occipital gyrus, calcarine sulcus, as well as right calcarine sulcus, superior parietal gyrus/intraparietal sulcus (putative areas LIP and VIP (Glasser et al. 2016)) and a small cluster in the right superior frontal lobe, see Figure 1*C*.

Third, we performed a RSA based on parameter estimates of each individual stimulus (see Methods) with the RDM of the semantic categories. This analysis revealed a significant correlation for a region in the lingual gyrus/calcarine sulcus as show in Figure 1*D*.

Relation Between Computational Features and Neural Activity

To address the hypothesis on the relation between cFeatures and neural activity, we looked separately at low- and mid-level features.

Low-Level Features

The RSA with the RDM of cAcceleration revealed a cluster of positive correlations in the left occipital pole/middle occipital gyrus, and the feature cMagneticOrientation revealed clusters of positive correlations in the left and right parieto-occipital sulcus, anterior V3 or V6, (see Fig. 2). cEnergy, and cGyro did not reveal any statistically significant results at the threshold used.

Mid-Level Features

The RSA with the RDM of cLightness revealed large clusters of positive correlation in the left and right supramarginal gyrus and the most posterior planum temporale, the left and right posterior STS as well as the left and right EBA regions (right MST/LO3 regions, the left MST/ FST, and LO3 regions) (see Fig. 3). The RSA with the RDM of cSymmetry revealed clusters of positive correlations in the left supramarginal gyrus (SMG), the most posterior temporal gyrus (pSTG), left EBA/hMT+, the left and right cuneus, the parieto-occipital sulcus, and the marginal sulcus. cPeriodicity did not reveal any statistically significant results.

The RDMs for the low- and mid-level cFeatures were somewhat correlated (see Fig. 4) but showed clusters in different regions, low-level cMagneticOrientation and cAcceleration features in early visual cortex (EV) and mid-level features cSymmetry and cLightness in OTC, SPL, IPL, and pSTG.

Relation Between Behavioral Features and Brain Activity

The RSA with the RDM of bMovement revealed large clusters of positive correlation in the left supramarginal gyrus, the very posterior planum temporale, the posterior STS and the anterior occipital sulcus, the right SMG, and the superior postcentral sulcus. The RSA with the RDM of bSymmetry revealed a cluster of positive correlation in the left occipital pole/middle occipital gyrus, (see Fig. 5).

Relation Between Computational Features and Behavioral Ratings

The behavioral ratings of the two stimulus categories showed that participants (not the same sample as the fMRI, see Methods) discriminated clearly between the two dance conditions (recognition accuracy for fragility = 81%, lightness = 80%).

As can be seen from the between RDM correlation matrix in Figure 4, cLightness was more similar to bMotion and bSymmetry than to any of the other computational features (see Fig. 4).

Regression RSA Analysis

An additional analysis was performed where the features were put together in a multilinear model, which is better able to account for shared variance between model RDMs and might therefore be able to distinguish unique contributions of model RDMs to neural activation patterns. Most of the results of the single feature RSA analyses were similar to this multilinear model; however, the set of regions in left OTC/IPL showed markedly different results. The feature bMotion showed a large cluster in right IPL and OTC as well as in medial SPL and medial

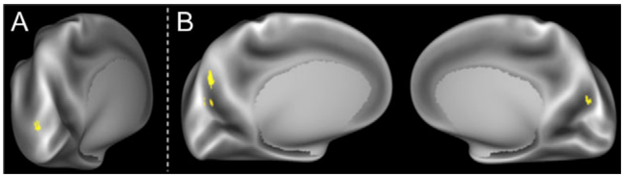

Figure 2. (*A*) Results of the second-level RSA of cAcceleration. (*B*) Results of the second-level RSA of cMagnetic Moment feature. Colors as in Figure 1.

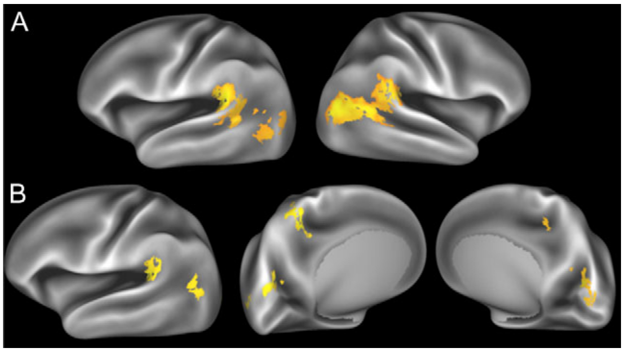

Figure 3. (*A*) Results of the second-level RSA with cLightness. (*B*) Results of the second-level RSA with the RDM of cSymmetry. Colors as in Figure 1.

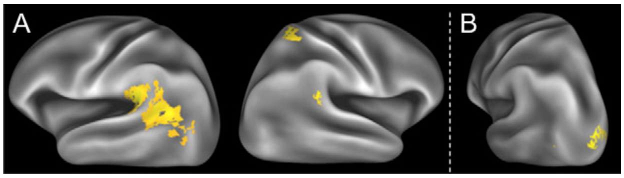

Figure 5. (*A*) Results of the second-level RSA with the RDM of the bMovement. (*B*) Results of the second-level RSA with the RDM of the bSymmetry. Colors as in Figure 1.

parietal gyrus. cLightness was similarly compared with the cLightness only analysis but had a significant cluster in EV. cSymmetry, in addition to the original results had a cluster in EV and clusters in medial and lateral superior parietal cortex. eActor was significant in most of the EV (see Fig. 6).

Discussion

Our goal was to use a computer model of movement features to gain a better understanding of the detailed brain mechanisms underlying movement perception in naturalistic videos. First, we identified brain activity that distinguishes between the two experimental variables of lightness and fragility. Second, we investigated how different computational features

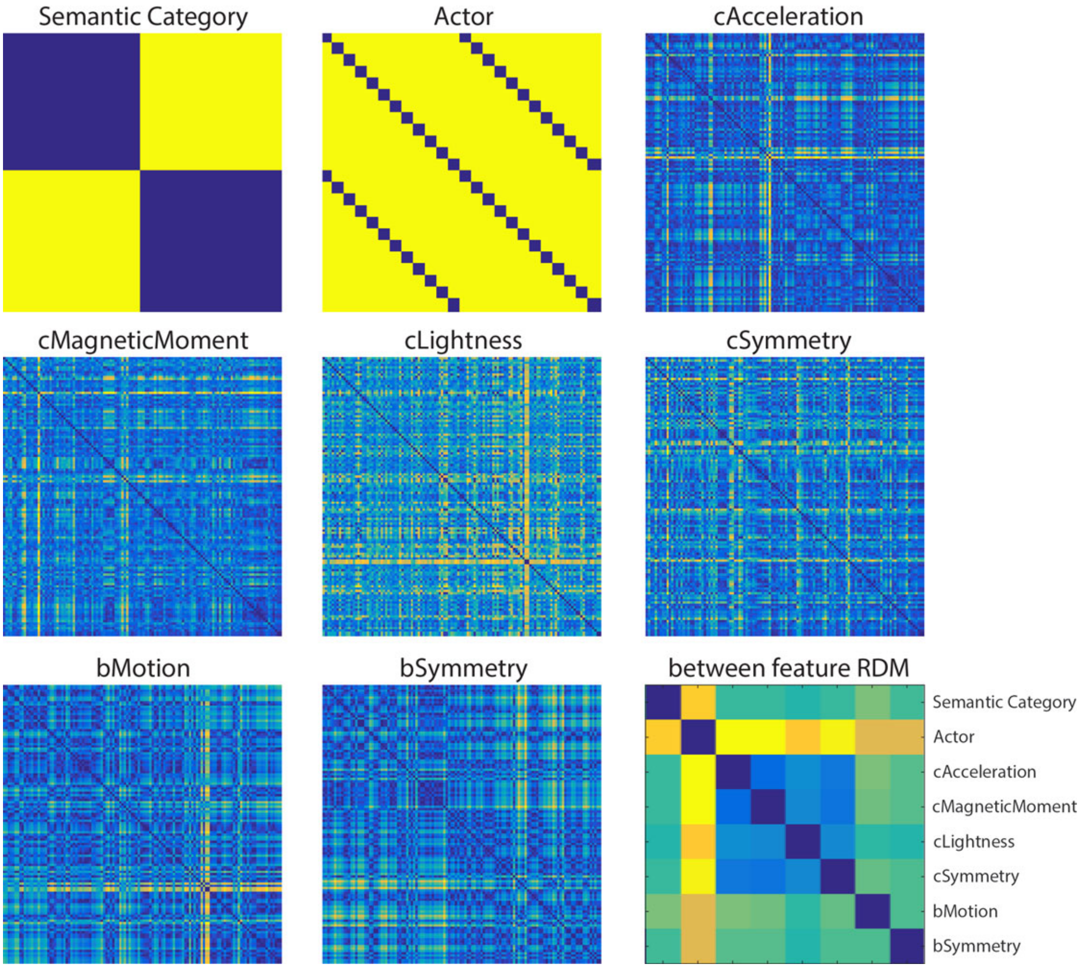

Figure 4. Matrix plot of the RDM's reported in the study and similarity between all used RDM's in the study (lower right panel). Color maps represent dissimilarities (1—Pearson's *r*-values, blue is similar, yellow is dissimilar), scaled per panel for best visualization.

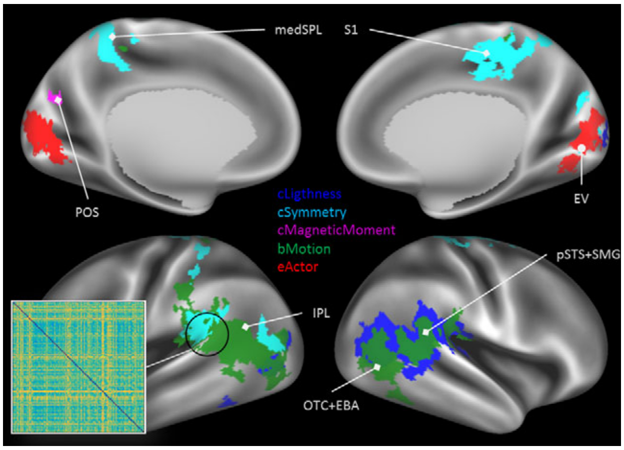

Figure 6. Overview of the regression RSA analysis. Regions indicated are medial superior, parieto-occipital gyrus (POS), parietal lobe (medSPL), somatosensory cortex (S1), EV, IPL, OTC, extrastriate body area (EBA), posterior superior temporal sulcus (pSTS), and SMG. Inset panel shows an example of the neural RDM from the regions in the pSTG.

of the bodily movements were related to brain activity. Then, we analyzed the relationship between the brain activity patterns for these three types of analysis in order to understand the how experimental variables, computational features, and behavioral ratings relate to each other and to brain activity.

Stimulus Category Discrimination

We found converging results of the three different analytical approaches used to find brain activation relating to the two experimental conditions. All three analyses revealed brain activation levels or patterns for a region in the lingual gyrus/calcarine sulcus as show in Figure 1*B*–*D*. In addition the GNB classifier also revealed a region in the SPL where the stimulus category could be decoded from brain activation patters. Activation in EV has been shown to contain decodable information about complex images and even is able to be used to predict what movie clips participant are viewing (Nishimoto et al. 2011). It is somewhat surprising that we do not find any higher level regions related to the experimental conditions, for instance in STS and frontal–parietal regions (Rizzolatti 2005; Urgesi et al. 2007). A possible explanation for this is that these regions are predominantly involved in body perception when the bodily action contains familiar actions, intentions, social relevance, or emotions (de Gelder 2016), while our stimuli contain abstract dance movements.

Brain Correlates of Computational Features

We investigated the neural basis of movement perception using low- and mid-level computational features. Our findings show that features belonging to two different levels of the computer model hierarchy map to different visual areas in early visual and in higher level motion-sensitive regions. The features that explicitly relate to dynamic aspects of posture were encoded in OTC/STS and SPL (see Fig. 5).

First, we found a relation between the model computational features and brain activation separately for low- and mid-level features. The low-level cFeatures cAcceleration, cMagneticMoment, and cSymmetry were related to activations in regions in the early visual hierarchy, mainly the superior medial parietal cortex and middle occipital gyrus, part of V3 and V6 (the dorsomedial area). cAcceleration mapped to the posterior part of V3, while cMagneticMoment and cSymmetry mapped to more anterior V3 and possibly V6 and the occipitoparietal sulcus. V3/V6/DM contains larger receptive fields than V1 and V2 and is tuned to coherent motion of large patterns covering extensive portions of the visual field (Braddick et al. 2001; Pitzalis et al. 2010). The dorsomedial area has been shown to map aspects of visual information that are relevant for motor control (Lui et al. 2006). The features of cAcceleration, cMagnetic moment, and cSymmetry are based upon motion of the wrists and are thus influenced by motion of the shoulders and up-down motion and rotation of the whole body. Hence, these features would map to patterns of optical flow at large visual fields.

cSymmetry and cLightness correlated with brain activity patterns in OTC and IPL. These regions are known to have functional specificity for bodies and body parts (Engelen et al. 2015), as well as biological motion (Decety and Grèzes 1999) and have previously been shown to elicit similar pattern of brain activity over participants passively viewing dance clips (Herbec et al. 2015; Reason et al. 2016). Interestingly, representational similarities were found for cSymmetry in both V3/V6, in OTC and IPL, indicating that this feature may be related to extensive posture/motion (and thus visual) differences as well as more abstract properties of body, limb, and biological motion. Symmetry is based on kinematic properties like energy and jerk, but importantly it is also linked to postural attributes relating the left to the right side of the body. Dissimilarity between stimuli on this level thus appears to be related to activity in regions that code for large field visual properties as well as regions that code for bodies, body parts, and biological motion (Giese and Rizzolatti 2015).

In contrast, cLightness was only related to OTC/IPL/pSTS activity and not to lower level regions in the visual cortex. This indicates that differences in lightness are mainly conveyed through more complex postural attributes that do not necessarily result in detectable dissimilarities in wide-field visual or optical flow patterns. The region in OTC for cLightness likely includes the EBA, which is known to be sensitive to whole body and body part images (Downing et al. 2001) and to movement as it is adjacent to hMT+/V5 (Ferri et al. 2013). It has also been suggested that EBA has independent neural populations for form and motion (Thompson and Baccus 2012), and that it interacts with dorsal parietal, sensori-motor and prefrontal regions to decode and predict complex movements. Interestingly, cLightness clusters in IPL/pSTS are also known to be a part of the ventral attention network (Corbetta and Shulman 2002). On the other hand, this cluster has also been specifically related to the subjective experience of illusory body ownership (Blanke 2012). Other researchers have arued that projecting oneself into another body has been related to the fact that action observation triggers activation in mirror neurons, presumably leading to motor contagion and sustaining emotional perception that could be a neural basis of esthetic experience (Freedberg and Gallese 2007). Along similar lines motor contagion has been viewed as the neural basis of higher order skills like empathy (Gallese et al. 2004). Whichever direction one wants to take, interpretations or motor contagion, the basic phenomenon of interest is that of a projection onto the seen body, a sensory identification with a body other than one's own. Interestingly, the notion of "getting into the skin of another" is traditionally viewed as a major aspect of artistic experience (Freedberg and Gallese 2007). The fact that IPL/TPJ emerges here in relation to a specific computational level of dance movement analysis seems to indicate that cLightness may be one of the features of the brain's computational mechanism that contributes to the spectator's identification with the dancer. As we will see, this tentative interpretation is supported by the finding of a neural overlap between cLighness and bMovement, discussed in the following.

Brain Correlates of Behavioral Features

The behavioral ratings for the features bSymmetry and bMotion were related to specific patterns of brain activation. In particular, bSymmetry mapped to V3 indicating that it relates to processing of basic visual features of the stimuli and not so much to more abstract dynamic or postural attributes. In contrast, bMotion was found to map to extensive regions in left OTC/EBA, bilateral SMG/angular gyrus, and right SPL. These are all regions known to be involved in biological motion perception or networks previously related to processes involved in action understanding (Rizzolatti et al. 2001). Possible subjective ratings of motion do take into account higher level and abstract notions of posture and interpretation of the intentions of the motions of the dancers. Right (and left) SPL has also been related to attending to motion and voluntary direction of attention (Thompson et al. 2005), and, in our context, might be related to bottom-up influences of attention to particularly interesting or salient movements of the dancers.

Relations Between Stimulus Categories, Computational and Behavioral Features

Our third aim was to understand how experimental conditions, computational features, and behavioral ratings relate to each other and to brain activity. Admittedly, this is a fundamental question for any approach that investigates brain activity guided by a computational model and not just by semantic categories. The present study makes a beginning with addressing these issues by showing partial correspondences between semantic categories, presumably transparent to the participants, used to describe dance categories (the experimental conditions), behavioral ratings, and on the other hand, the model features derived from computational feature analysis. Overall, our study illustrated the important point that the relation between natural behavior and neural activity patterns is very complex (Krakauer et al. 2017). One does not expect that behavioral ratings of movement characteristic can be reduced to computational model features or the other way round. A first indication is that the individual behavioral ratings of the stimulus characteristics (bFeatures) do not seem to clearly separate the two experimental categories. This suggests that recognition of eLightness and eFragility cannot be reduced to one or another one specific movement characteristic of the behavioral ratings. Importantly, we found that when all bFeatures were combined in a single RDM, this indeed yielded a clear distinction between the two categories, (see Supplementary Fig. 2). Combined with the fact that participants performed classification of the categories with high accuracy, this suggests that participants use a combination of low-level features to (passively) recognize different movement patterns. This pattern may mimic the different levels of the model features.

Concerning the relation between computational features and features from behavioral ratings, we found substantial overlap between them but only in some brain regions. First, bSymmetry mapped to V3, close to the results of the GNB classifier, the RSA with category and the RSA with cAcceleration. Indeed, the RDM of bSymmetry reveals a good separation between the two dance conditions and this may then explain that the GNB classifier and the RSA with categories map to this same region. Next, the RSA of bMotion overlapped substantially with the RSA of cLightness. Here also, from the constituent RDM's, it can be seen that some of the stimuli that stand out for cLightness are also rated very dissimilar to other stimuli on bMotion. Indeed, the region (EBA, or including EBA) in the OTC where cLightness, bMotion, and cSymmetry (left only) overlap has previously been found in a study where computational parameters as well as behavioral parameters of a dance video covary with the BOLD signal (Noble et al. 2014).

The multilinear regression RSA is able to account for shared variance between model RDM's and might therefore be better able to distinguish unique contributions of model RDM's to neural activation patterns. This analysis revealed that many of the results seen in the EV could be explained by shared variance between several model RDM's and the actor RDM, as the multilinear regression model clearly revealed that the actor RDM accounted for most variance in EVC. Our initial results showed that a number of RDM's were significantly correlated with activation in left OTC/IPL; however, the multilinear regression model revealed that the bMotion accounted for most of the shared variance. Even though some of the features displayed no supra-threshold RSA results, we found that including these features in the regression RSA model enhanced the significance of the features bMotion, cLightness, and cSymmetry. This most likely indicates that even though their corresponding activity is sub-threshold, these other features account for some meaningful variance in the fMRI signal.

In conclusion, by using a model based on features for analyzing brain activity, we reveal specific functional roles of different brain areas involved in different features of movement. Our approach illustrates how one can go beyond classical methods of categorically mapping cognitive constructs to brain activation/deactivation by providing details of the underlying feature-based brain mechanisms. Our findings suggest that body movement perception is organized in the brain not so much by semantic categories than by feature statistics of the movement. Behavioral features based on subjective ratings of movement have a patchy relation with the computational features. Future research along these lines should focus on understanding the complex relation between the brain mechanisms of movement perception and subjective experience.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Notes

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