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Distinct functional roles of the mirror neuron system and the mentalizing system

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ABSTRACT

Movements can inform us about what people are doing and also about how they feel. This phenomenologically evident distinction has been suggested to correspond functionally with differential neural correlates denoted as mirror neuron system (MNS) and mentalizing system (MENT). To separate out the roles of the underlying systems we presented identical stimuli under different task demands: character animations showing everyday activities (mopping, sweeping) performed in different moods (angry, happy). Thirty-two participants were undergoing functional magnetic resonance imaging (fMRI) while asked to identify either the performed movement or the displayed mood. Univariate GLM analysis revealed the expected activation of either in MNS or MENT depending on the task. A complementary multivariate pattern-learning analysis based on the "social brain atlas" confirmed the expected recruitment of both systems. In conclusion, both approaches converge onto clearly distinct functional roles of both social neural networks in a novel dynamic social perception paradigm.

1. Introduction

Nonverbal communication constitutes an essential part of human social interactions (Mehrabian and Wiener, 1967). It is characterized by a high dimensional complexity due to its multichannel nature implying the simultaneous presentation of a variety of cues, such as smiles, gaze, hand gestures, postures and body movement (Bente et al., 2008; Kuzmanovic et al., 2011; Vogeley and Bente, 2010). Among the different nonverbal cue systems, whole-body movement has proved to be an extremely rich information source. Not only does it reveal both the function and goal of an observed action (Dittrich, 1993), it also provides clues to the inner experience of persons including their moods (Atkinson et al., 2004; Aviezer et al., 2012; Clarke et al., 2005; Pollick et al., 2001). In this sense, we use movement information to identify not only what people are actually doing, but also how they are doing it, respectively in which mood they are acting. In fact, these are fundamentally different cognitive tasks to perform, but both are necessary to successfully navigate our social world and to effectively communicate and collaborate with others.

In social neuroscience, two different brain systems are discussed as neural correlates of social information processing: the "mirror neuron system" (MNS) and the "mentalizing system" (MENT; also designated as "theory of mind system"). The MNS is recruited not only during one's own movements, but also during the observation of others' movements, corresponding to the original electrophysiological finding of increased firing rates of mirror neurons during action execution and action observation (di Pellegrino et al., 1992; Gallese et al., 1996). The much more ambitious claim that the MNS also contributes to the complex capacity of "action understanding", either based on an automatic process of "resonance" induced in the observer during the observation of a movement (Rizzolatti et al., 2001) or based on "direct matching" (Rizzolatti and Sinigaglia, 2010) or on "simulation" (Gallese and Goldman, 1998; Gallese et al., 2004) has been a matter of substantial debate (Hickok, 2009, 2014; Caramazza et al., 2014).

In contrast, MENT allows humans to attribute inner mental states to

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other persons, such as thoughts, emotions, moods, or intentions (Amodio and Frith, 2006; Frith and Frith, 2003). MENT is specifically recruited when inner mental states including emotions and intentions have to be inferred from human motion (Blake and Shiffrar, 2007; de Lange et al., 2008; Spunt et al., 2011, 2010; Spunt and Lieberman, 2012a, 2012b; Troje, 2013). Until now, only a few studies investigated MNS and MENT within the same approach. For instance, a moving object in changing environmental contexts allowed different interpretations either of an inanimated object (associated with MNS activation) or an animated, selfpropelled agent (associated with MENT activation) (Wheatley et al., 2007). The perception of animated stimuli expressing personhood recruited MENT in contrast to MNS that was associated with being prepared to read out potentially socially salient information (Santos et al., 2010). Focusing on the neural correlates of the movement kinematics ("how") and the motivation to perform the actions ("why") key regions of MENT showed increased neural activation during the identification of motivational states ("why"), whereas the left occipito-temporal cortex was associated with the identification of "how" the action was performed (Spunt et al., 2011, 2010; Spunt and Lieberman, 2012a).

On this empirical basis, the hypothesis has been proposed that MNS serves comparably early stages of social information processing related to the "detection" of spatial or bodily signals such as movements, whereas MENT is recruited during comparably late stages of social information processing related to the "evaluation" of inner experiences of others (Vogeley, 2017). Interestingly, the fundamental distinction of MNS and MENT has also been shown recently by the "social brain atlas" obtained from about 4,000 empirical studies in social neuroscience in a fully data-driven, meta-analytic integration (Alcalá-López et al., 2017). Based on connectivity modeling, evaluating both coactivation in task-focused brain states and physiological fluctuations, and exploring correlations in task-free brain states 36 key regions responsible for social information processing were identified. Notably, a hierarchical cluster analysis of the functional connectivity of all 36 brain regions revealed that the most basic differentiation of all regions separates between two groups of regions that resemble MNS and MENT (Alcalá-López et al., 2017).

In this study we address the question whether the two different functional roles of detection of movements and evaluation of mood can be attributed to MNS and MENT. For this purpose, the same stimuli of a newly developed paradigm were presented with two different instructions. Furthermore, classical univariate analysis was complemented by identifying the contribution of both systems by leveraging multivariate machine-learning algorithms on the basis of the social brain atlas (Alcalá-López et al., 2017). The traditional univariate approach in imaging neuroscience is based on the classical null-hypothesis testing framework, which explores the whole brain and evaluates pairs of contrasts or groups of individuals (Friston et al., 1994). In contrast, out-of-sample pattern generalization can profit from starting with regions-of-interest (ROIs) to guide extraction of multivariate patterns of neural activity changes on an interpretable target atlas. Such statistical learning methodology aims to decode cognitive processes from neural activity by training pattern-learning algorithms on a larger share of brain scans after which the predictive performance is evaluated in an independent part of functional neuroimaging data (Bzdok, 2017).

To the best of our knowledge, this is the first study that makes use of a coherent and homogeneous stimulus set that is psychophysically well characterized and that is used to explore both MNS and MENT by means of identical stimuli in both conditions. The major objectives of our study are two-fold. First, we wanted to characterize the functional roles of MNS and MENT by asking for the identification of movements (hypothesized to be associated with MNS activation) and for the identification of moods during the performance of the movement (hypothesized to be associated with MENT activation). Second, this is the first empirical validation of the social brain atlas (Alcalá-López et al., 2017) that is exploited for the purpose of a multivariate analysis complementing a classical univariate approach. The complementary combination of univariate inference of significant task contrasts and multivariate generalization of recruitment combinations predictive of tasks substantially contributes from an analytical perspective to our research question.

2. Material and methods

2.1. Participants

Participants were included, if they were right-handed according to a standard handedness inventory (EHI (Oldfield, 1971), had normal or corrected to normal vision, had no history of psychiatric or neurological disease and were not taking any neuro- or psychotropic medication. All participants were naïve to the purpose of the study. Prior to the experiment, each participant provided written informed consent to participate in the study. Procedures were approved by the ethics committee of the Medical Faculty of the University of Cologne. Three participants had to be excluded because of low task-performance during the fMRI scanning. 32 volunteers were included in the data analysis (17 males; mean age: 25.75 ± 4.91 years standard deviation (SD)).

2.2. Design of the stimulus material

For the generation of the stimuli, an independent group of 31 individuals, naïve for the purpose of the study, none of which a professional actor, was recruited (14 males; mean age: 25.55 ± 6.01 years SD). These participants were asked to perform a series of 6 different movements (sweeping the floor, mopping the floor, wiping a table with a rag, sanding a piece of wood on a table, painting a wall with a brush, painting a wall with a roller) in 3 different moods (angry happy, sad). For the purpose of this study we later selected stimuli showing two different movements (sweeping, mopping) in two different moods (happy, angry). In order to let persons execute the different movements as natural as possible while displaying the different moods, a mood induction procedure and specific instructions were used (Lammers, 2017). Instructions were presented as audio recordings. Movements of all participants were recorded by a motion capture system (Optitrack™, NaturalPoint, Inc., Oregon, USA). Using the commercially available software systems Maya™ and MotionBuilder™ (Autodesk Inc., California, USA) the motion capture recordings were translated to video sequences presenting wooden mannequins as humanoid avatars (Fig. 1). Video sequences of 5 s were cut out of the total recorded video sequence of approx. 30 s. Before accepting any video as suitable stimulus for this study, it was psychophysically studied in detail. In particular, we checked pixel change and velocity of the movements and excluded outliers to guarantee comparability of stimuli with respect to physical characteristics in the kinematic of the displayed body movements (Lammers, 2017). For the objective analysis of the kinematic trajectories of the movements we used an algorithm

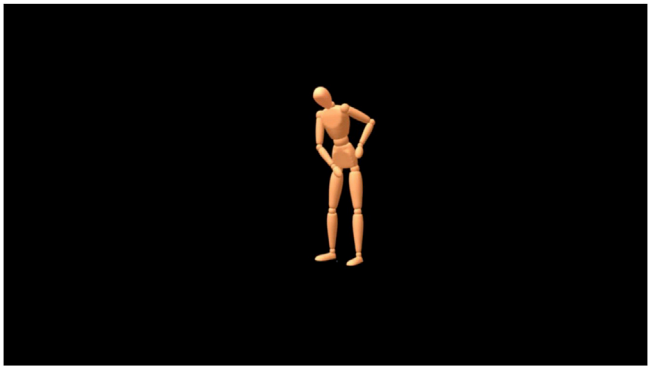

Fig. 1. Avatar standstill.
Standstill of an animated video sequence showing a wooden mannequin as avatar performing mopping. Animated videos were presented showing one out of two different movements (sweeping, mopping) combined with one out of two moods (happy, angry) resulting in four different types of video animations.

implemented in Matlab (R2017a; The MathWorks, Inc., Natick, USA) by one of the authors (RT). In particular, videos sequences were analyzed frame by frame as pixel intensity changes. As all avatar movements take place in a certain ROI also the frame to frame changes of the horizontal and vertical extent and the change of the ROI area had been analyzed. Any repetitive movement is reflected by periodical patterns in the videos with a certain frequency and amplitude, representing the velocity of a movement and the magnitude of movement changes, respectively. Frequency and amplitude data were also considered to quantify the characteristics of movements.

On the basis of these analyses we were able to select a homogeneous set of animated video sequences excluding outliers in any of the above mentioned variable (with outlier defined as a value outside the range of mean ± 2 x SD in any variable). The remaining videos were then tested in an online study to measure the recognition rates for movement and mood. To this end we recruited 112 volunteers (39 males; mean age: 31.66 ± 11.71 years SD). The majority of videos were rated 60–100% correctness (Lammers, 2017, Table 1). For the final stimulus set we selected video sequences that showed similar recognition rates for both, movement and mood. As a result of these procedures we were able to put together a collection of animated videos that at the same time contained information about the performed movement and the presented mood. In order to probe movement detection and mood evaluation we used 32 video sequences in four different combinations (sweeping-happy, sweeping-angry, mopping-happy, mopping-angry). Formally, this design constituted a 2 x 2 two-factorial design with 2 factors (movement, mood) and 2 different levels each (movement: sweeping, mopping; mood: happy, angry). As we had no strong hypothesis for the difference between both movements or both moods and as the differentiation of movements and moods was used as experimental vehicle to study the differential neural correlates of processing movement- and mood-related information, we focused on this research question only and did not study the differential effects between the two particular movements and the two moods on a neural level.

Table 1
Stimulus material.

Video Nr.	Movement	Mood	Recognition Rate Movement	Recognition Rate Mood
01	mopping	angry	52	68
02	mopping	angry	78	36
03	mopping	angry	63	84
04	mopping	angry	84	73
05	mopping	angry	68	94
06	mopping	angry	78	42
07	mopping	angry	84	57
08	mopping	angry	73	84
09	mopping	happy	84	78
10	mopping	happy	73	78
11	mopping	happy	84	94
12	mopping	happy	68	42
13	mopping	happy	89	94
14	mopping	happy	84	73
15	mopping	happy	78	78
16	mopping	happy	100	84
17	sweeping	angry	89	78
18	sweeping	angry	89	63
19	sweeping	angry	68	52
20	sweeping	angry	89	78
21	sweeping	angry	73	63
22	sweeping	angry	78	42
23	sweeping	angry	68	68
24	sweeping	angry	100	100
25	sweeping	happy	84	73
26	sweeping	happy	89	57
27	sweeping	happy	84	94
28	sweeping	happy	47	63
29	sweeping	happy	63	63
30	sweeping	happy	73	89
31	sweeping	happy	78	57
32	sweeping	happy	84	89

This table provides information about the different stimuli employed in this study. Exactly 50% of all stimuli showed “sweeping” or “mopping” with respect to the presented movement and “happy” or “angry” mood with respect to the inscribed mood. Stimuli were presented from different angles. Recognition by all test persons participating in the fMRI study are provided in percent.

2.3. Procedure

The experiment was analyzed as block design to acquire strong and robust signals to answer the key question of differential neural correlates during processing movement- and mood-related information. Both conditions of movement detection and mood evaluation followed exactly the same procedure during the experiment in order to make both conditions as comparable as possible. Stimuli were shown in a simple blockwise fashion with 4 trials per block. In each block we presented a general instruction first (either the word “TÄTIGKEIT” (“MOVEMENT”) or “STIMMUNG” (“MOOD”), after that 4 stimuli of 5 s each were shown followed by a response window of 3 s each, all stimuli of a given block had to be judged either according to the binary choice of movements or to the binary choice of moods. The experiment consisted of 16 blocks of 4 trials each, leading to 64 trials for the whole experiment. After a general instruction before the experiment, specific short instructions were presented in the beginning of each block for 3 s (either “TÄTIGKEIT, engl. “MOVEMENT”, or “STIMMUNG”, engl. “MOOD”). If the instruction “MOVEMENT” was presented, participants had to identify the movement. If the instruction "MOOD" was presented, participants had to identify the mood of the person depicted by the avatar. Subsequently, a block of 4 trials commenced. The rules alternated periodically within one session; 16 participants started with the instruction “MOOD”, whereas 16 started with the instruction “MOVEMENT”.

Every trial consisted of a silent animated video sequence with a duration of 5 s, showing a wooden mannequin (Fig. 1) performing one of the four different combinations of movement and mood (sweeping-happy, sweeping-angry, mopping-happy, mopping-angry). After each video sequence, a simple forced-choice was required with two different response options that were presented for 3 s consisting of one word on the left and right side of the screen. If the instruction “TÄTIGKEIT” (engl. “MOVEMENT”) was depicted, participants had to choose between "FEGEN" (engl. "SWEEPING") and "WISCHEN" (engl. "MOPPING"). If the instruction “STIMMUNG” (engl. “MOOD”) was presented, participants had to decide between "GLÜCKLICH" (engl. "HAPPY") or "WÜTEND" (engl. "ANGRY"). Left or right positions for the responses were systematically counterbalanced. Participants were requested to position and keep their hands on two LumiTouch devices (Photon Control Inc., Burnaby, BC, Canada) with their left and right index fingers on the response button of both response devices. Participants were asked to press the spatially corresponding button of the word (left or right) that described the movement or mood of the video sequence best. After the response, a jitter of 1–2 s was inserted before the next trial began. Every block lasted about 41 s with a subsequent resting period as baseline lasting for 10–11 s (uniformly jittered).

Stimuli were presented using Psychopy (version: 1.84.2; Peirce, 2009) and were displayed on a custom-built, shielded TFT screen at the rear end of the fMRI scanner, visible via a mirror mounted on the headcoil. Participants did not receive training prior to performing the task inside the scanner nor did they get any feedback during the experiment. Motor responses were recorded via LumiTouch devices during the fMRI session. For all subjects, an accuracy score (number of correct trials divided by 32 trials) for both conditions (i.e., MOVEMENT and MOOD) was computed. A one-sample *t*-test was conducted to compare accuracy scores for both conditions.

2.4. fMRI data acquisition

Brain images were acquired on a Siemens 3-T Trio MRI scanner (Erlangen, Germany) using blood oxygen level-dependent (BOLD)

contrast (Gradient-echo, T2* EPI pulse sequence, TR = 2200 ms, 36 axial slices, 3 mm thickness, interslice distance of 15%, 64 x 64 image matrix, FoV 200 mm, voxel size of 3.1 x 3.1 × 3.0 mm^3) covering the whole brain. For the main experiment, 420 volumes were acquired using an interleaved slice mode. Four dummy images were considered to allow for magnetic field saturation, which were discarded prior to further processing.

2.5. Classical mass-univariate analysis of task contrasts

Brain images were analyzed using SPM12 (Statistical Parametric Mapping; Wellcome Department of Imaging Neuroscience, London, United Kingdom; www.fil.ion.ucl.ac.uk/spm), implemented in Matlab 9.0 (The MathWorks, Inc., Natick, USA). After the images were corrected for head movements using realignment, the mean EPI image for each subject was mapped on the individual anatomical MRI. The mean EPI as well as the anatomical MRI were coregistered to the Montreal Neurological Institute (MNI) reference space using the unified segmentation algorithm in SPM12. Functional images were then spatially smoothed using a 10 mm FWHM Gaussian kernel to meet the statistical requirements of further analyses and to compensate for macroanatomical interindividual differences across participants. The data were analyzed using a general linear model (GLM) as implemented in SPM12. Two onset regressors were defined reflecting the two different experimental conditions MOVEMENT and MOOD. Duration was set to 38 s to cover the period from the beginning of the first video sequence until the end of the fourth response window. A third regressor was used to separate blocks with more than two errors (either wrong answers or misses).

The hemodynamic response was modeled using a canonical hemodynamic response function and its first time derivative. The six head movement parameters were included as confounding variables (Lund et al., 2005). For first-level analyses, simple main effects for each experimental condition were computed by applying appropriate baseline contrasts. To account for inter-subject variability in the group analysis, the contrast images obtained at the first-level were included in a second-level *t*-test to create an SPM map. Since we wanted to study the different neural activity while processing the two conditions MOVEMENT and MOOD, we calculated differential contrasts for the MOVEMENT and MOOD conditions (i.e. MOVEMENT > MOOD; MOOD > MOVEMENT). All fMRI statistics were corrected by using a statistical threshold of $p < 0.05$, familywise error-corrected (FWE). Activated brain regions were defined as clusters consisting of more than 20 continuous voxels. The anatomical localization of the activated brain regions were defined anatomically using i) the SPM Anatomy Toolbox (Eickhoff et al., 2005) for those regions that have been cytoarchitectonically mapped, and ii) the Anatomical Labeling atlas (Tzourio-Mazoyer et al., 2002).

2.6. Multivariate analysis of task contrasts using social brain atlas

The univariate regression contrast analyses were subsequently complemented by revisiting the task fMRI data using multivariate pattern-learning algorithms. The whole-brain fMRI data were summarized based on the recently established social brain atlas (Alcalá-López et al., 2017). For each brain map acquired during task response, we have obtained 36 brain locations of interest that were shown to exhibit consistent recruitment in healthy subjects across a large variety of social-affective experiment classes, read out from nearly 4,000 empirical studies and more than 22,000 participants. We used the scikit-learn package executed in Python because it provides efficient, unit-tested implementations of state-of-the-art machine learning algorithms (http://scikit-learn.org). This general-purpose machine-learning library was interfaced with the nilearn library for design and efficient execution of neuroimaging data analysis workflows ("http://github.com/nilearn/nilearn"). The whole-brain neural activity information was summarized by averaging each brain map by spheres (radius = 5 mm) around each of the 36 regions in the social brain atlas. We used binary masks in which the neural activity information from all voxels of the sphere, corresponding to a particular social brain region, were aggregated and then summarized by computing the across-voxel average for each sphere of the social brain atlas. This approach yielded a feature space of the form number of task images x number of social brain regions. These data were unit-scaled to a variance of 1 and mean centered to 0 to avoid scale-invariance effects. The ensuing reexpression of whole-brain neural activity information in a neurobiological meaningful target atlas was fed into a maximum-margin linear support vector machine (C hyperparameter was kept at default 1). Model fitting and evaluation was based on the cross-validation gold standard to obtain an unbiased estimate of the expected out-of-sample prediction performance (Hastie et al., 2001). In 10 data-split iterations (i.e 10-fold cross-validation scheme), the data were divided into 90% training set used to train the learning algorithm on the social brain engagements and 10% testing set where the obtained pattern classifier was benchmarked for its performance that we would expect in new participants (Bzdok, 2017). This pattern-learning approach enabled the identification of those nodes of the predefined social brain atlas regions most relevant to distinguish MNS and MENT scenarios in the experimental study.

3. Results

3.1. Behavioral data

In contrast to the behavioral pilot data (Lammers, 2017; Lammers et al., under review), results revealed a significant difference between the accuracy scores ($t(31) = 5.218$, $p < 0.001$) with higher accuracy when the identification of correct movement out of two possible answers was requested (sweeping, mopping; condition MOVEMENT; ($81.15 \pm 9.31\%$) compared to the identification of the correct mood out of two possible answers (happy, angry; condition MOOD; $68.07 \pm 11.69\%$), suggesting that the identification of the performed movement was easier for the population of test persons studied under fMRI conditions compared to the identification of the presented mood.

3.2. Neural data: univariate analysis

For the analysis of neural responses we only included blocks with a sufficient performance rate of accuracy of 75% or 100% corresponding to 3 or 4 correct responses out of 4 required responses. We studied the main effects of MOVEMENT (MOVEMENT > MOOD; Fig. 2a; Table 2) and MOOD (MOOD > MOVEMENT; Fig. 2b; Table 2) that survived the statistical threshold of $p = 0.05$, familywise error-corrected (FWE) and the cluster threshold of more than 20 continuous voxels.

For the main effect of MOVEMENT, we found increased neural activity in the superior frontal gyrus (SFG), the left and right dorsal premotor cortex (dPMC) extending to the superior frontal gyrus (SFG), the anterior part of the left supramarginal gyrus, the inferior parietal lobule (aIPL), bilateral superior parietal lobule with the anterior part of the left and right intraparietal sulcus (aIPS), the left middle temporal gyrus including the left-sided, posterior part of the superior temporal sulcus (pSTS). Detailed localisations are depicted in Fig. 2a and provided in Table 2.

The main effect of MOOD showed increased activation in the dorsal part of the bilateral medial prefrontal cortex (dmPFC), the SFG bilaterally, the right superior medial gyrus, left orbitofrontal cortex including the anterior part of the inferior frontal gyrus (aIFG), the left medial temporal pole including the anterior part of the superior temporal sulcus (aSTS) and left angular gyrus, which is also included in the temporoparietal junction (TPJ). Detailed localisations are depicted in Fig. 2a and provided in Table 2.

3.3. Neural data: multivariate analysis based on the social brain atlas

In the multivariate data-analysis setting, the statistical analysis

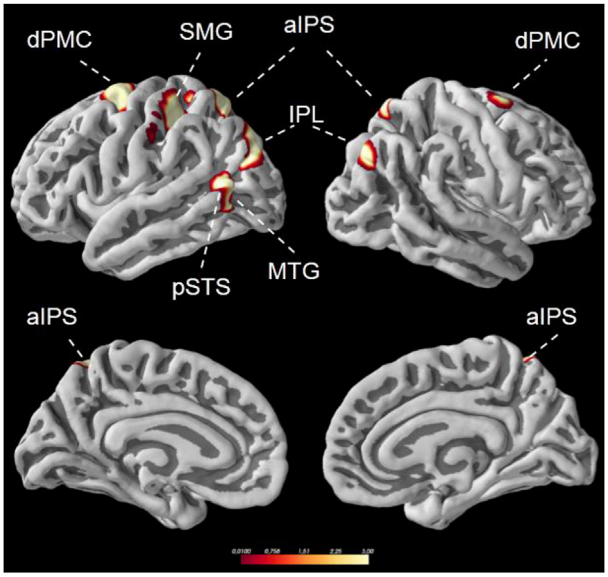

Fig. 2a. Univariate Analysis: Movement vs Mood.
Brain regions that were recruited during the detection of the correct movement, comprising the left and right dorsal premotor cortex (dPMC), the anterior part of the left supramarginal gyrus (SMG), the inferior parietal lobule (aIPL), bilateral superior parietal lobule with the anterior part of the left and right intraparietal sulcus (aIPS), the left middle temporal gyrus (MTG) including the left-sided, posterior part of the STS (pSTS) (Siemens 3T, SPM12, block design, n = 32, random effect, threshold p = 0.05, FWE corr.).

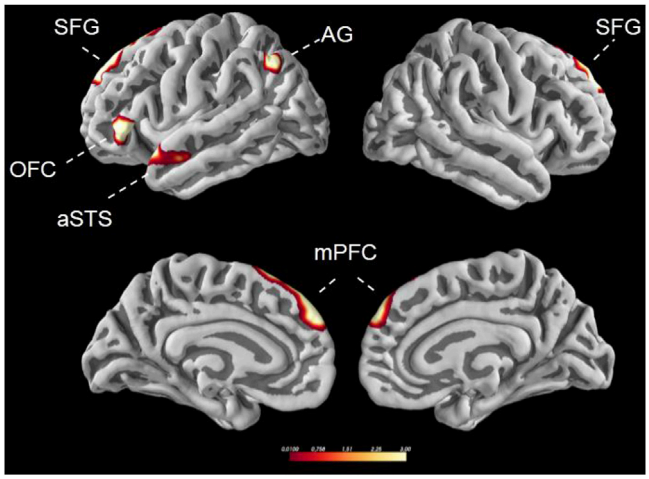

Fig. 2b. Univariate Analysis: Mood vs Movement.
Brain regions that were recruited during the evaluation of the correct mood, comprising the dorsal part of the bilateral medial prefrontal cortex (dPFC), the superior frontal gyrus (SFG) bilaterally, the right superior medial gyrus, left orbitofrontal cortex (OFC) including the anterior part of the inferior frontal gyrus, the left medial temporal pole including the anterior part of the superior temporal sulcus (aSTS) and left angular gyrus (AG), which is also included in the temporo-parietal junction (Siemens 3T, SPM12, block design, n = 32, random effect, threshold p = 0.05, FWE corr.).

considered only information locally from the predefined social brain atlas. The pattern-learning algorithm could reliably distinguish the two different experimental conditions of our study, namely MOVEMENT and MOOD, based on neural activity in the 36 target regions of the social brain atlas with an overall accuracy of 65.22% ± 3.30% (chance level 50%). Such prediction performance is quite reasonable given that the here probed cognitive classes are higher cognitive functions that tend to be more challenging to capture by predictive algorithms (Haynes, 2015; Horoufchin et al., 2018; Saygin et al., 2011). This is the classification performance that we would expect in new participants undergoing the study who were not part of the current data sample. The classification approach i) demonstrates that the social brain regions are contributing with different degrees to the networks recruited during processing of the two different conditions of MOVEMENT and MOOD, and ii) allows for insight into which nodes of the social brain are most informative for the distinction of both conditions. In particular, the rostral anterior cingulate cortex, left MT+/V5, and posterior cingulate cortex were most informative for the recognition of the MOVEMENT condition. In contrast, the recruitment of the dorsomedial prefrontal cortex, left inferior frontal gyrus, and left temporal pole are most informative for the identification of the MOOD condition. It is noteworthy that the bilateral amygdala, the anterior and posterior mid to cingulate cortex as well as the pSTS on the left side were among the least task-predictive regions. Such findings, however, do not exclude significant task-contrast effects.

4. Discussion

We aimed to show that the processing of human motor behavior recruits distinct neural systems depending on the instruction. We hypothesized that the detection of movement or functional classification of motor behavior would recruit key regions of MNS, while the evaluation

Table 2
Main effects for MOVEMENT and MOOD.

Contrast	Region Label	Cluster Size	t-Value	MNI Coordinates		
				x	y	z
Movement > Mood	Superior Frontal Gyrus	303	9,35	−20	0	56
	Supramarginal Gyrus	680	8,11	−44	−32	42
	aIPL left		7,00	−64	−22	30
	Superior Parietal Lobule	846	7,71	−18	−60	58
	aIPS left		7,52	−32	−72	22
	Middle Temporal Gyrus	318	7,65	−50	−60	−4
	Superior Parietal Lobule	65	6,84	16	−62	52
	aIPS right	76	6,61	38	−72	26
	Superior Frontal Gyrus	58	6,41	22	6	60
Mood > Movement	Superior Frontal Gyrus	1878	10,20	−14	52	34
	mPFC left		8,00	−6	32	58
	mPFC right		7,66	16	56	38
	Frontal Orbital Cortex	215	7,54	−50	30	−10
	Medial Temporal Pole	93	6,68	−50	10	−26
	Angular Gyrus	101	6,57	−54	−60	34

Peak activations observed in whole-brain analysis for the contrasts MOVEMENT (MOVEMENT > MOOD) and MOOD (MOOD > MOVEMENT). All activations reached a significance threshold of $p < 0.05$ (FWE). Coordinates x, y, z refer to Montreal Neurological Institute (MNI) coordinates in the left-right, anterior-posterior, and inferior-superior dimension respectively, t-value refers to the t-score at those coordinates (local maxima).

of mood or the inference of moods inscribed to the performed movements would predominantly recruit MENT (Vogeley, 2017). To this end, we introduced a novel paradigm, which allows to direcly compare neural activity under different task affordances with exactly the same stimuli. Beyond that we used a multivariate analysis based on the social brain atlas that examines the degree to which the predefined brain regions can predict activation associated with both tasks. Results of both analytical strategies, namely standard univariate analysis of the group of participants and the social brain atlas approach, show a substantial convergence. Our initial hypothesis about the different functional roles of MNS (physical detection of movement) and MENT (evaluation of moods) was confirmed. By showing that both types of information are inscribed in human movements and that they can elicit the recruitment of the fundamentally distinct neural systems this study goes substantially beyond the current state of knowledge in social neuroscience.

4.1. Converging evidence for the neural basis of detection and evaluation

To contribute to a more complete understanding of the functional roles of MNS and MENT in the domain of social neuroscience, we have made use of a newly developed paradigm in which we use a homogeneous and psychophysically well characterized stimulus set that provides a window into jointly addressing two different cognitive processes. This is to the best of our knowledge the first study that provides clear evidence for differential neural activation in both systems depending on the task. To further substantiate our findings in the social brain, we directly compared univariate and multivariate approaches. As key results, the dPMC and the inferior parietal lobe (IPL) were identified as contributing to the movement task and, hence, the MNS in both analytical approaches. The ventral part of the mPFC and the posterior part of the cingulate cortex (PCC) were apparent as combined with the other discriminatory atlas regions to allow task detection in the multivariate approach probing relevant combinations of social brain regions, but were not found to be statistically significant in the univariate region-by-region approach when studying the movement task (cf. this review (Bzdok, 2017)). In contrast, the dorsal part of the mPFC, the IFG, the left temporal pole and the bilateral TPJ were identified by both approaches during the mood evaluation task, whereas the PCC was only identified when seeking region combinations to discriminate the experimental conditions in the multivariate approach, but was not evaluted to be statistically significant at the employed threshold in the univariate approach during mood evaluation. It is interesting to note that the amygdala bilaterally, the middle part of the cingulate gyrus and the left pSTS do not contribute in any way to the differentiation of both functional systems suggesting a similar contribution to both tasks (Fig. 2a and b; Fig. 3a). The relative contribution of social brain key nodes is provided in Fig. 3b.

As key result, we observe a substantial convergence when we compare task-responsive brain regions in the univariate and multivariate approaches. The corresponding results of both methods essentially corroborate the existence of two different functional systems that can be robustly elicited by the two different tasks of movement detection and mood evaluation. The traditional imaging neuroscience approach to generate rigorous conclusions from experimental data is based on classical statistical inference, which is typically used in neuroimaging to explore the whole brain and evaluate groups of persons, cognitive contrasts are calculated by separate GLM models for each individual voxel in the brain, finally significant differences between the calculated coefficients for each task condition (Friston et al., 1994). In contrast, out-of-sample pattern generalization can profit from starting with ROIs that provide direct neurobiological meaningful observation units and guide extraction of multivariate patterns of neural activity changes. In so doing, the statistical learning methodology does not only estimate model coefficients to brain activity of a given sample of participants but aims to decode cognitive processes from neural activity signals in individuals that would be observed in the future. This is done by training pattern-learning algorithms on the large basis of the social brain atlas on the foundation of which the predictive performance is evaluated in an independent part of functional neuroimaging data of this particular study (Bzdok, 2017). Our multivariate predictive patterns that held up out-of-sample based approach learned task-distinctive activation patterns based on *combinations* of neural activity changes in the nodes of the social brain for decoding the cognitive processes from fMRI signals (Bzdok, 2017). As a result, both approaches, univariate statistical inference and multivariate out-of-sample pattern generation, contribute in a complementary manner to the goal of our study.

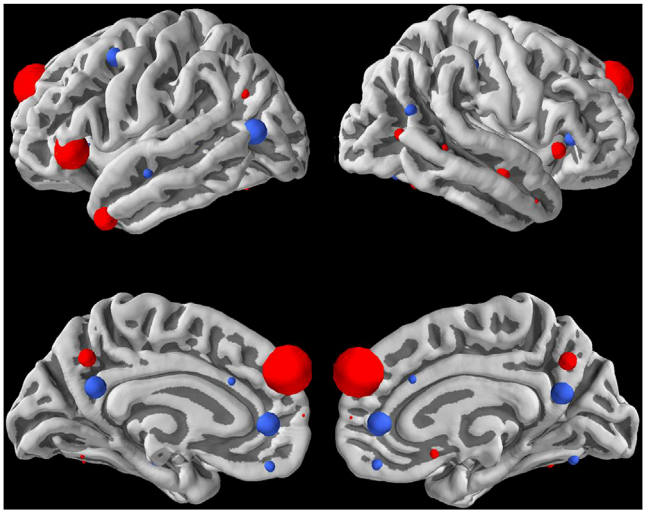

Fig. 3a. Multivariate analysis.
Identification of relevant nodes of the social brain atlas and their contribution to the two different tasks (detection of movement, recruiting MNS, blue; evaluation of mood, recruiting MENT, red; size of the spheres corresponds to the strength of their contribution to the network). Results show a substantial overlap with univariate analyses (Fig. 2a and b) but also marked differences.

4.2. Detection of movements ("what?") recruits the mirror neuron system

Converging evidence in both types of analyses is demonstrated for the dPMC and the IPL during the movement task (Figs. 2a and 3a). These three regions are involved in motor planning, including both premotor and primary motor cortex (Grezes, 1998; Hamilton et al., 2006; Raos et al., 2004; Santi et al., 2003). The recruitment of MNS during the perceptual processing of actions in movements confirms previous studies focusing on action observation (Spunt et al., 2010, 2011; Spunt and Lieberman, 2013). The detected so-called action observation network shows a high overlap with MNS in general (Georgescu et al., 2014).

The visual input during the observation of actions is presumably processed in the PMC and compared to one's own repertoire of motor programs, subsequently, in case of a match, the actions' goal is identified (Desmurget et al., 2009; Iacoboni et al., 2005; Lau et al., 2004; Rizzolatti et al., 2001). Functionally closely linked to PMC and also aIPS is the superior temporal sulcus (STS) that is responsive to facial motion, hand actions, and body movements (Allison et al., 2000; Nishitani and Hari, 2002). The pSTS is involved in the identification of biological motion and intentionality, whereas its more anterior part is responsible for identifying motion in general (Allison et al., 2000). These two regions of the PMC and pSTS were also recruited when experienced dancers were watching other dancers (Calvo-Merino et al., 2005) indicating that familiarity of the observed action plays an important role. Functional knowledge of a tool, like household aids in our study, provoke action knowledge which activates the IPS, IPL and dPMC (Canessa et al., 2008; Kellenbach et al., 2003). Finally, from a clinical perspective, a lesion of the IPL often leads to apraxia that includes the impairment in the proper usage of objects (Binder et al., 2017; Rothi and Heilman, 1997).

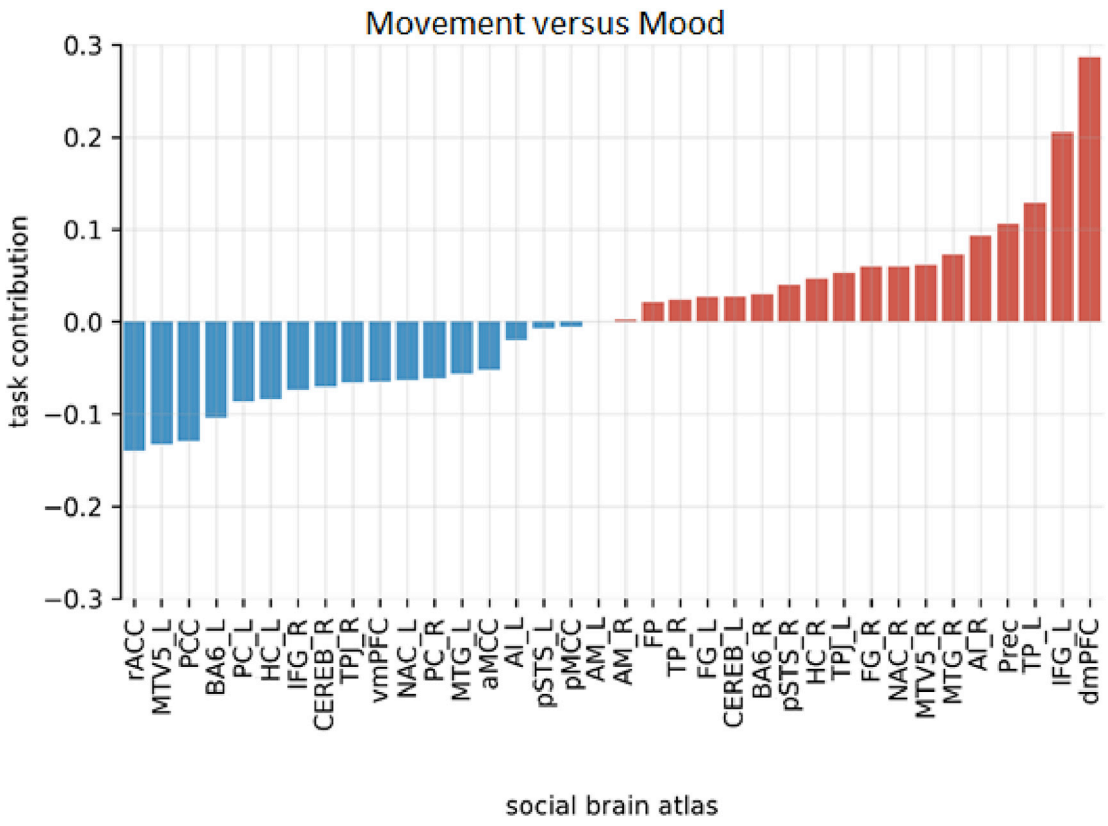

Fig. 3b. Relative contribution of social brain key nodes to the tasks and systems.
All 36 brain regions of the social brain atlas (x-axis) are ordered along their relative weight or contribution to the performance of the two tasks (detection of movement, recruiting MNS, blue; evaluation of mood, recruiting MENT, red). Analogous to linear regression analysis, the relevance of each social brain region was assigned a negative (blue) or positive (red) weight. The overall 'decision' of whether a given brain scan belongs to a given experimental condition was derived from the weighted sum of the 36 social brain nodes. As such, each of these 36 relative region contributions can be interpreted as pulling the decision towards one or the other condition, holding the remaining 35 region contributions constant. Whereas the dmPFC contributes most substantially to the performance of the mood evaluation task, the right ACC contributes most to the performance of the movement detection task; some regions including the amygdala bilaterally are uninformative with respect to the differentiation of both tasks and systems, respectively.

4.3. Evaluation of moods ("how?") recruits the mentalizing system

In contrast, the dorsal part of the mPFC, the IFG, the temporal pole on the left side and the TPJ were identified by both approaches during the mood evaluation task. This subset of regions corresponds to MENT (Decety and Lamm, 2007; Desmurget and Sirigu, 2009; Frith and Frith, 2003) (Fig. 2b; Fig. 3a). The purpose of MENT is to contribute to the proper understanding, explanation or prediction of the behavioral agenda of others on the basis of their goals and inner mental states (de Lange et al., 2008; Grèzes et al., 2004; Spunt et al., 2011, 2010; Spunt and Lieberman, 2012b). This confirms previous studies providing evidence for the contributions of the mPFC, the TPJ, the posterior cingulate cortex/precuneus (PC), the IFG, and both the anterior as well as the posterior part of the STS (aSTS, pSTS) (Amodio and Frith, 2006; Frith and Frith, 2003; Gallagher et al., 2000; Mitchell, 2006; Saxe, 2006; Vogeley et al., 2001).

Especially the mPFC has been reported to be involved in the detection of emotions (Etkin et al., 2011) and processing of emotional mentalizing tasks (Krause et al., 2012). It is also active in the empathic concern of other person's affective state (Shamay-Tsoory and Aharon-Peretz, 2007; Völlm et al., 2006) and in reflective reasoning about actions and judgments including goals and intentions (de Lange et al., 2008; Van der Cruyssen et al., 2009). Meta-analytical approaches have shown that the dorsal part of the mPFC (dmPFC) was selectively associated with perspective-taking and episodic memory retrieval which is intimately related to the task of our study when a judgment of the presented mood was required. This can be understood as "top–down-driven, probabilistic-scene-informed, and metacognition-related processing in social cognition" based on functional connections with the inferior frontal gyrus, the temporo-parietal junction, and the middle temporal gyrus (Bzdok et al., 2013a,b). Similarly, the middle zone of the mPFC was found to be associated with cognitive control, pain, and affect processing (de la Vega et al., 2016). Also the IFG was reported consistently associated with social cognition including processes that underpin emotional contagion and emotion recognition (Nummenmaa et al., 2008; Schurz et al., 2014).

Further corroborated is this interpretation by the involvement of both mPFC and IFG in emotional contagion and emotion recognition: Jabbi et al., (2007) have reported that observing facial expressions activated parts of the IFG. In addition, in the cited study, participants' empathic performance scores were predictive of their IFG activation while witnessing facial expressions. As already stated above, discussing the correlates of movement detection, the pSTS is involved in the identification of biological motion, social cues and the underlying intentionality (Allison et al., 2000; Frith and Frith, 1999; Morris et al., 2005) and, hence, the social significance of actions (Iacoboni et al., 2004). Via functional connections with the amygdala (Adolphs, 1999), one could assume that STS activation is modulated by the emotional cues of an action (LaBar et al., 2003). The activation of the aSTS is in line with other studies investigating mentalizing (Brunet et al., 2000; Castelli et al., 2000; Gallagher et al., 2000). Especially the pSTS can not be clearly distinguished from the TPJ that is assumed to play a fundamental role during processing of goals and intentions (Saxe and Powell, 2006). An interesting speculation was proposed by Van Overwalle (Van Overwalle,

2009), namely that the TPJ is mainly responsible for transient mental inferences about people such as their goals, desires and beliefs, whereas the mPFC subserves the attribution of more general traits and qualities about the self and other people. He also suggests that the TPJ could be a core hub mediating the dynamic link between MNS and MENT due to its selective involvement in goal inferences and the connection to the aIPS, a key region in the MNS (Bzdok et al., 2013a; Mars et al., 2012). Our results, however, go substantially beyond these studies as they show that both types of informations that are relevant for the interpretation of movements and the inner experience of the agent inscribed to the movement are ready for readout.

4.4. Two complementary social networks

Based on our own data we propose the complementarity of both networks in social information processing according to which the MNS serves the "detection" of spatial or bodily signals such as movements, whereas MENT is recruited during the "evaluation" of inner experiences of others such as moods (Vogeley, 2017). This interpretation is in good concordance with a series of studies that focused on both systems in a comparable fashion. In two studies addressing animacy it was shown that inaminate objects appearing as "physical" were associated with MNS activity as opposed to animate, self-propelled objects appearing as "personal" revealed MENT activation (Wheatley et al., 2007; Santos et al., 2010). Key regions of MENT were also activated if the motivational states "behind" or inscribed in movements ("why") were to be evaluated as opposed to the judgement of movement kinematics ("how"; Spunt et al., 2011, 2010; Spunt and Lieberman, 2012a). The fundamental neurobiological distinction between both systems has also been corroborated meta-analytically on the basis of hierarchical cluster analysis based on connecitivity patterns of 36 key regions underlying social cognition (Alcalá-López et al., 2017).

This complementary relation of both systems that appear to interact with each other during the processing of socially relevant information argues explicitly against the speculation that the MNS is responsible - besides the undisputable involvement in action execution and action observation - not only for action understanding (Rizzolatti et al., 2001; Rizzolatti and Sinigaglia, 2010), but also for the interpretation of emotions and empathy (Gallese and Goldman, 1998; Gallese et al., 2004). A few authors have claimed that the MNS also contributes to the high-level process of "action understanding", an automatic, pre-reflexive, non-inferential process of the premotor cortex during the observation of movements, also referred to as "resonance" (Rizzolatti et al., 2001), "direct matching" (Rizzolatti and Sinigaglia, 2010) or "simulation" (Gallese and Goldman, 1998; Gallese et al., 2004). However, a number of critical objections can be raised against this view that the high-level process of action understanding is constituted by the low-level process of matching action observation and action execution (Hickok, 2009, 2014; Caramazza et al., 2014).

With respect to the role of MNS in action understanding, the activity of mirror neurons being sensitive to the visual presentation of different kinds of actions (e.g. Umiltà et al., 2001; Fogassi et al., 2005) is relevant. Here it has been argued that an alternative explanation is possible according to which the necessary action categorizations required for action understanding are generated in other brain regions and that these non-motor representations of the different actions are only retrieved by mirror neurons. We found in our study IPL activation which could also be interpreted as component of the dorsal visual stream, that is held responsible for sensorimotor transformations for visually guided actions towards objects (Goodale and Milner, 1992). In further support of this view, studies on the human MNS demonstrated that the processing of action representations is not restricted to early motor areas (Caramazza et al., 2014). In other words, the nature of the link between sensory and motor information is unclear. This becomes even more obvious when mirror neurons respond to comparably poor sensory data, e.g. acoustic (e.g. cracking a peanut) instead of visual cues (Kohler et al., 2002). Such an acoustic cue does not allow a direct error-free association of a movement in the sense of "direct matching" (Rizzolatti and Sinigaglia, 2010) but appears to require a more complex categorization elsewhere in the brain before this association can be retrieved by the MNS (Caramazza et al., 2014).

Another objective is that action execution is not necessary for action understanding, "the ability to understand actions does not require the ability to execute them" (Hickok, 2014, p. 48) as in the cases of limb apraxia or Moebius syndrome. Action understanding and action execution dissociate in humans, individuals with upper limb dysplasia were shown to be able to "perceive, anticipate, predict, comprehend and memorize" actions of the upper limb actions which they were physically not able not simulate (Vannuscorps and Caramazza, 2016).

The ascription of a role in the processing of emotions and mind-reading to the MNS (Gallese and Goldman, 1998; Gallese et al., 2004) appears to be clearly over-emphasized, it was argued that the activity of mirror neurons represent "a primitive version, or possibly a precursor in phylogeny, of a simulation heuristic that might underlie mind-reading" (Gallese and Goldman, 1998, p. 498) or that allow "the experiential understanding of the emotions of others." (Gallese et al., 2004, p. 396). Our data can be read as arguing against this strong position as we can show that MNS is not recruited during the ascription of internal states to others, even if they are inscribed to movements and can not be identified other than by inferring them from the movement of the observed persons. The presentation of the stimuli did not provide any kind of information that could have supported any kind of attribution of mental states based on previous knowledge of the observed person, the context or any other information not inscribed in the movement. In other words, our data clearly provide evidence against the strong claim that the MNS provides "a neurophysiological account of the experiential dimension of both action and emotion understanding" (Gallese et al., 2004, p. 396)."

4.5. Limitations

As we present an fMRI experiment, we can only study relative differences in activity of the two systems. In particular, it is possible that in the mood evaluation condition also MNS was recruited in a less pronounced way. In addition, we have to emphasize that moods can never be ultimately confirmed and need to be inferred by the individual based on tentative evidence, such as any mental stance of other individuals. Results of the behavioral data show that the accuracy of the emotion perception was significantly lower than for the action perception. This difference could lead to altered neural activation in the brain due to higher cognitive load. However, it is important to note that the mood evaluation was more difficult to assign to the stimuli for the population participating in the fMRI study, so at least we can state that the corresponding neural results are not confounded by resting state-like mind-wandering or daydreaming (Smallwood and Schooler, 2006).

5. Conclusion

In this fMRI study, we provide an explicit demonstration that movement detection and mood evaluation are statistically distinguishable in their recruitment of MNS and MENT as two fundamentally distinct systems of the complex construct of the social brain. This conclusion could only be drawn on the basis of an experimental setup like this in which exactly the same stimulus material was used during two different mindsets: This clearly shows that the mood-related information is already present in the way *how* we perform a movement in addition to the information *what* movement is performed. Notably, both experimental tasks and task-responsive cohesive brain systems respectively, could be complementarily identified by the univariate as well as the multivariate approaches undertaken. This successful localization for the first time provides an experimental vehicle to rigorously study the interaction of both systems in the near future. It is, for instance, of foremost interest to better understand which kind of stimuli or which parameter stimulate the

MNS and which elicit activation in MENT. Related to this is the need to better understand both systems on a much more detailed time scale, e.g. employing technologies with high temporal resolution like magnetoencephalography (MEG). Furthermore, this study design is also well suited to explore the differential contributions of both systems to different psychopathologies. For instance, it is well known that persons with autistic traits show impairments in the identification of emotions.

Conflicts of interest

The authors declare no competing financial interests.

References

Adolphs, R., 1999. Social cognition and the human brain. Trends Cogn. Sci. 3, 469–479.

Alcalá-López, D., Smallwood, J., Jefferies, E., Van Overwalle, F., Vogeley, K., Mars, R.B., Turetsky, B.I., Laird, A.R., Fox, P.T., Eickhoff, S.B., Bzdok, D., 2017. Computing the social brain connectome across systems and states. Cerebr. Cortex 28, 2207–2232. https://doi.org/10.1093/cercor/bhx121.

Allison, T., Puce, A., McCarthy, G., 2000. Social perception from visual cues: role of the STS region. Trends Cogn. Sci. 4, 267–278.

Amodio, D.M., Frith, C.D., 2006. Meeting of minds: the medial frontal cortex and social cognition. Nat. Rev. Neurosci. 7, 268–277. https://doi.org/10.1038/nrn1884.

Atkinson, A.P., Dittrich, W.H., Gemmell, A.J., Young, A.W., 2004. Emotion perception from dynamic and static body expressions in point-light and full-light displays. Perception 33, 717–746. https://doi.org/10.1068/p5096.

Aviezer, H., Trope, Y., Todorov, A., 2012. Body cues, not facial expressions, discriminate between intense positive and negative emotions. Science 338, 1225–1229. https://doi.org/10.1126/science.1224313.

Bente, G., Senokozlieva, M., Pennig, S., Al-Issa, A., Fischer, O., 2008. Deciphering the secret code: a new methodology for the cross-cultural analysis of nonverbal behavior. Behav. Res. Methods 40, 269–277.

Binder, E., Dovern, A., Hesse, M.D., Ebke, M., Karbe, H., Saliger, J., Fink, G.R., Weiss, P.H., 2017. Lesion evidence for a human mirror neuron system. Cortex 90, 125–137. https://doi.org/10.1016/j.cortex.2017.02.008.

Blake, R., Shiffrar, M., 2007. Perception of human motion. Annu. Rev. Psychol. 58, 47–73. https://doi.org/10.1146/annurev.psych.57.102904.190152.

Brunet, E., Sarfati, Y., Hardy-Baylé, M.C., Decety, J., 2000. A PET investigation of the attribution of intentions with a nonverbal task. Neuroimage 11, 157–166. https://doi.org/10.1006/nimg.1999.0525.

Bzdok, D., 2017. Classical statistics and statistical learning in imaging neuroscience. Front. Neurosci. 11, 543. https://doi.org/10.3389/fnins.2017.00543.

Bzdok, D., Langner, R., Schilbach, L., Jakobs, O., Roski, C., Caspers, S., Laird, A.R., Fox, P.T., Zilles, K., Eickhoff, S.B., 2013a. Characterization of the temporo-parietal junction by combining data-driven parcellation, complementary connectivity analyses, and functional decoding. Neuroimage 81, 381–392. https://doi.org/10.1016/j.neuroimage.2013.05.046.

Bzdok, D., Langner, R., Schilbach, L., Engemann, D.A., Laird, A.R., Fox, P.T., Eickhoff, S.B., 2013b. Segregation of the human medial prefrontal cortex in social cognition. Front. Hum. Neurosci. 7, 232.

Calvo-Merino, B., Glaser, D.E., Grèzes, J., Passingham, R.E., Haggard, P., 2005. Action observation and acquired motor skills: an FMRI study with expert dancers. Cerebr. Cortex 15, 1243–1249. https://doi.org/10.1093/cercor/bhi007.

Canessa, N., Borgo, F., Cappa, S.F., Perani, D., Falini, A., Buccino, G., Tettamanti, M., Shallice, T., 2008. The different neural correlates of action and functional knowledge in semantic memory: an FMRI study. Cerebr. Cortex 18, 740–751. https://doi.org/10.1093/cercor/bhm110.

Caramazza, A., Anzellotti, S., Strnad, L., Lingnau, A., 2014. Embodiment cognition and mirror neurons: a critical assessment. Annu. Rev. Neurosci. 37, 1–15.

Castelli, F., Happé, F., Frith, U., Frith, C., 2000. Movement and mind: a functional imaging study of perception and interpretation of complex intentional movement patterns. Neuroimage 12, 314–325. https://doi.org/10.1006/nimg.2000.0612.

Clarke, T.J., Bradshaw, M.F., Field, D.T., Hampson, S.E., Rose, D., 2005. The perception of emotion from body movement in point-light displays of interpersonal dialogue. Perception 34, 1171–1180. https://doi.org/10.1068/p5203.

de Lange, F.P., Spronk, M., Willems, R.M., Toni, I., Bekkering, H., 2008. Complementary systems for understanding action intentions. Curr. Biol. 18, 454–457. https://doi.org/10.1016/j.cub.2008.02.057.

de la Vega, A., Chang, L.J., Banich, M.T., Wager, T.D., Yarkoni, T., 2016. Large scale meta-analysis of human medial frontal cortex reveals tripartite functional organization. J. Neurosci. 36, 6553–6562.

Decety, J., Lamm, C., 2007. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. The Neuroscientist 13, 580–593. https://doi.org/10.1177/1073858407304654.

Desmurget, M., Reilly, K.T., Richard, N., Szathmari, A., Mottolese, C., Sirigu, A., 2009. Movement intention after parietal cortex stimulation in humans. Science 324, 811–813. https://doi.org/10.1126/science.1169896.

Desmurget, M., Sirigu, A., 2009. A parietal-premotor network for movement intention and motor awareness. Trends Cogn. Sci. 13, 411–419. https://doi.org/10.1016/j.tics.2009.08.001.

di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. Exp. Brain Res. 91, 176–180.

Dittrich, W.H., 1993. Action categories and the perception of biological motion. Perception 22, 15–22. https://doi.org/10.1068/p220015.

Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25, 1325–1335. https://doi.org/10.1016/j.neuroimage.2004.12.034.

Etkin, A., Egner, T., Kalisch, R., 2011. Emotional processing in anterior cingulate and medial prefrontal cortex. Trends Cogn. Sci. 15, 85–93. https://doi.org/10.1016/j.tics.2010.11.004.

Fogassi, L., Ferrari, P.F., Gesierich, B., Rozzi, S., Chersi, F., Rizzolatti, G., 2005. Parietal lobe: from action organization to intention understanding. Science 308, 662–667.

Friston, K.J., Holmes, A.P., Worsley, K.J., Poline, J.-P., Frith, C.D., Frackowiak, R.S.J., 1994. Statistical parametric maps in functional imaging: a general linear approach. Hum. Brain Mapp. 2, 189–210. https://doi.org/10.1002/hbm.460020402.

Frith, C.D., Frith, U., 1999. Interacting minds–a biological basis. Science 286, 1692–1695.

Frith, U., Frith, C.D., 2003. Development and neurophysiology of mentalizing. Philos. Trans. R. Soc. Lond. B Biol. Sci. 358, 459–473. https://doi.org/10.1098/rstb.2002.1218.

Gallagher, H.L., Happé, F., Brunswick, N., Fletcher, P.C., Frith, U., Frith, C.D., 2000. Reading the mind in cartoons and stories: an fMRI study of 'theory of mind' in verbal and nonverbal tasks. Neuropsychologia 38, 11–21.

Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. Brain 119, 593–609.

Gallese, V., Goldman, A., 1998. Mirror neurons and the simulation theory of mind-reading. Trends Cogn. Sci. 2, 493–501.

Gallese, V., Keysers, C., Rizzolatti, G., 2004. A unifying view of the basis of social cognition. Trends Cogn. Sci. 8, 396–403.

Georgescu, A.L., Kuzmanovic, B., Santos, N.S., Tepest, R., Bente, G., Tittgemeyer, M., Vogeley, K., 2014. Perceiving nonverbal behavior: neural correlates of processing movement fluency and contingency in dyadic interactions. Hum. Brain Mapp. 35, 1362–1378. https://doi.org/10.1002/hbm.22259.

Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. Tr. Neurosci. 15, 20–25.

Grezes, J., 1998. Top down effect of strategy on the perception of human biological motion: a pet investigation. Cogn. Neuropsychol. 15, 553–582. https://doi.org/10.1080/026432998381023.

Grèzes, J., Frith, C., Passingham, R.E., 2004. Brain mechanisms for inferring deceit in the actions of others. J. Neurosci. 24, 5500–5505. https://doi.org/10.1523/JNEUROSCI.0219-04.2004.

Hamilton, A.F. de C., Wolpert, D.M., Frith, U., Grafton, S.T., 2006. Where does your own action influence your perception of another person's action in the brain? Neuroimage 29, 524–535. https://doi.org/10.1016/j.neuroimage.2005.07.037.

Hastie, T., Tibshirani, R., Friedman, J., 2001. The Elements of Statistical Learning. Springer, Heidelberg, Germany.

Haynes, J.-D., 2015. A primer on pattern-based approaches to fMRI: principles, pitfalls, and perspectives. Neuron 87, 257–270. https://doi.org/10.1016/j.neuron.2015.05.025.

Hickok, G., 2009. Eight problems for the mirror neuron theory of action understanding in monkeys and humans. J. Cogn. Neurosci. 21, 1229–1243.

Hickok, G., 2014. The Myth of Mirror Neurons. The Real Neuroscience of Communication and Cognition. W. W. Norton & Company, New York, London.

Horoufchin, H., Bzdok, D., Buccino, G., Borghi, A.M., Binkofski, F., 2018. Action and object words are differentially anchored in the sensory motor system - a perspective on cognitive embodiment. Sci. Rep. 8, 6583. https://doi.org/10.1038/s41598-018-24475-z.

Iacoboni, M., Lieberman, M.D., Knowlton, B.J., Molnar-Szakacs, I., Moritz, M., Throop, C.J., Fiske, A.P., 2004. Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. Neuroimage 21, 1167–1173. https://doi.org/10.1016/j.neuroimage.2003.11.013.

Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G., 2005. Grasping the intentions of others with one's own mirror neuron system. PLoS Biol. 3. https://doi.org/10.1371/journal.pbio.0030079.

Jabbi, M., Swart, M., Keysers, C., 2007. Empathy for positive and negative emotions in the gustatory cortex. Neuroimage 34, 1744–1753. https://doi.org/10.1016/j.neuroimage.2006.10.032.

Kellenbach, M.L., Brett, M., Patterson, K., 2003. Actions speak louder than functions: the importance of manipulability and action in tool representation. J. Cogn. Neurosci. 15, 30–46. https://doi.org/10.1162/089892903321107800.

Kohler, E., Keysers, C., Umiltà, M.A., Fogassi, L., Gallese, V., Rizzolatti, G., 2002. Hearing sounds, understanding actions: action representation in mirror neurons. Science 297, 846–848.

Krause, L., Enticott, P.G., Zangen, A., Fitzgerald, P.B., 2012. The role of medial prefrontal cortex in theory of mind: a deep rTMS study. Behav. Brain Res. 228, 87–90. https://doi.org/10.1016/j.bbr.2011.11.037.

Kuzmanovic, B., Schilbach, L., Lehnhardt, F.G., Bente, G., Vogeley, K., 2011. A matter of words: impact of verbal and nonverbal information on impression formation in high-functioning autism. Res. Autism Spectr. Disord. 5, 604–613. https://doi.org/10.1016/j.rasd.2010.07.005.

LaBar, K.S., Crupain, M.J., Voyvodic, J.T., McCarthy, G., 2003. Dynamic perception of facial affect and identity in the human brain. Cerebr. Cortex 13, 1023–1033.

Lammers, S., 2017. Production and Perception of Whole-Body Movements to Probe the Social Brain (B.Sc. Thesis). University of Cologne, Cologne, Germany. Retrieved from. https://doi.org/10.31237/osf.io/swucv.

Lau, H.C., Rogers, R.D., Haggard, P., Passingham, R.E., 2004. Attention to intention. Science 303, 1208–1210. https://doi.org/10.1126/science.1090973.

Lund, T.E., Nørgaard, M.D., Rostrup, E., Rowe, J.B., Paulson, O.B., 2005. Motion or activity: their role in intra- and inter-subject variation in fMRI. Neuroimage 26, 960–964.
Mars, R.B., Neubert, F.-X., Noonan, M.P., Sallet, J., Toni, I., Rushworth, M.F.S., 2012. On the relationship between the "default mode network" and the "social brain". Front. Hum. Neurosci. 6. https://doi.org/10.3389/fnhum.2012.00189.
Mehrabian, A., Wiener, M., 1967. Decoding of inconsistent communications. J. Personal. Soc. Psychol. 6, 109–114.
Mitchell, J.P., 2006. Mentalizing and Marr: an information processing approach to the study of social cognition. Brain Res. 1079, 66–75. https://doi.org/10.1016/j.brainres.2005.12.113.
Morris, J.P., Pelphrey, K.A., McCarthy, G., 2005. Regional brain activation evoked when approaching a virtual human on a virtual walk. J. Cogn. Neurosci. 17, 1744–1752. https://doi.org/10.1162/089892905774589253.
Nishitani, N., Hari, R., 2002. Viewing lip forms: cortical dynamics. Neuron 36, 1211–1220.
Nummenmaa, L., Hirvonen, J., Parkkola, R., Hietanen, J.K., 2008. Is emotional contagion special? An fMRI study on neural systems for affective and cognitive empathy. Neuroimage 571–580. https://doi.org/10.1016/j.neuroimage.2008.08.014.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113. https://doi.org/10.1016/0028-3932(71)90067-4.
Peirce, J.W., 2009. Generating stimuli for neuroscience using PsychoPy. Front. Neuroinf. 2. https://doi.org/10.3389/neuro.11.010.2008.
Pollick, F.E., Paterson, H.M., Bruderlin, A., Sanford, A.J., 2001. Perceiving affect from arm movement. Cognition 82, B51–B61.
Raos, V., Evangeliou, M.N., Savaki, H.E., 2004. Observation of action: grasping with the mind's hand. Neuroimage 23, 193–201. https://doi.org/10.1016/j.neuroimage.2004.04.024.
Rizzolatti, G., Fogassi, L., Gallese, V., 2001. Neurophysiological mechanisms underlying the understanding and imitation of action. Nat. Rev. Neurosci. 2, 661–670. https://doi.org/10.1038/35090060.
Rizzolatti, G., Sinigaglia, C., 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. Nat. Rev. Neurosci. 11, 264–274.
Rothi, L.J., Heilman, K.M., 1997. Apraxia: the Neuropsychology of Action. Psychology Press.
Santi, A., Servos, P., Vatikiotis-Bateson, E., Kuratate, T., Munhall, K., 2003. Perceiving biological motion: dissociating visible speech from walking. J. Cogn. Neurosci. 15, 800–809. https://doi.org/10.1162/089892903322370726.
Santos, N.S., Kuzmanovic, B., David, N., Rotarska-Jagiela, A., Eickhoff, S.B., Shah, J.N., Fink, G.R., Bente, G., Vogeley, K., 2010. Animated brain: a functional neuroimaging study on animacy experience. Neuroimage 53, 291–302. https://doi.org/10.1016/j.neuroimage.2010.05.080.
Saxe, R., 2006. Uniquely human social cognition. Curr. Opin. Neurobiol. 16, 235–239. https://doi.org/10.1016/j.conb.2006.03.001.
Saxe, R., Powell, L.J., 2006. It's the thought that counts: specific brain regions for one component of theory of mind. Psychol. Sci. 17, 692–699. https://doi.org/10.1111/j.1467-9280.2006.01768.x.
Saygin, Z.M., Osher, D.E., Koldewyn, K., Reynolds, G., Gabrieli, J.D.E., Saxe, R.R., 2011. Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. Nat. Neurosci. 15, 321–327. https://doi.org/10.1038/nn.3001.
Schurz, M., Radua, J., Aichhorn, M., Richlan, F., Perner, J., 2014. Fractionating theory of mind: a meta-analysis of functional brain imaging studies. Neurosci. Biobehav. Rev. 42, 9–34. https://doi.org/10.1016/j.neubiorev.2014.01.009.
Shamay-Tsoory, S.G., Aharon-Peretz, J., 2007. Dissociable prefrontal networks for cognitive and affective theory of mind: a lesion study. Neuropsychologia 45, 3054–3067. https://doi.org/10.1016/j.neuropsychologia.2007.05.021.
Smallwood, J., Schooler, J.W., 2006. The restless mind. Psychol. Bull. 132, 946–958. https://doi.org/10.1037/0033-2909.132.6.946.
Spunt, R.P., Falk, E.B., Lieberman, M.D., 2010. Dissociable neural systems support retrieval of how and why action knowledge. Psychol. Sci. 21, 1593–1598. https://doi.org/10.1177/0956797610386618.
Spunt, R.P., Lieberman, M.D., 2012a. An integrative model of the neural systems supporting the comprehension of observed emotional behavior. Neuroimage 59, 3050–3059. https://doi.org/10.1016/j.neuroimage.2011.10.005.
Spunt, R.P., Lieberman, M.D., 2012b. Dissociating modality-specific and supramodal neural systems for action understanding. J. Neurosci. 32, 3575–3583. https://doi.org/10.1523/JNEUROSCI.5715-11.2012.
Spunt, R.P., Lieberman, M.D., 2013. The busy social brain: evidence for automaticity and control in the neural systems supporting social cognition and action understanding. Psychol. Sci. 24, 80–86. https://doi.org/10.1177/0956797612450884.
Spunt, R.P., Satpute, A.B., Lieberman, M.D., 2011. Identifying the what, why, and how of an observed action: an fMRI study of mentalizing and mechanizing during action observation. J. Cogn. Neurosci. 23, 63–74. https://doi.org/10.1162/jocn.2010.21446.
Troje, N., 2013. What is biological motion? Definition, stimuli, and paradigms. In: Rutherford, M.D., Kuhlmeier, V.A. (Eds.), Social Perception: Detection and Interpretation of Animacy, Agency, and Intention. MIT Press, pp. 13–36. https://doi.org/10.7551/mitpress/9780262019279.003.0002.
Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. Neuroimage 15, 273–289. https://doi.org/10.1006/nimg.2001.0978.
Umiltà, M.A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., Rizzolatti, G., 2001. I know what you are doing: a neurophysiological study. Neuron 31, 155–165.
Van der Cruyssen, L., Van Duynslaeger, M., Cortoos, A., Van Overwalle, F., 2009. ERP time course and brain areas of spontaneous and intentional goal inferences. Soc. Neurosci. 4, 165–184. https://doi.org/10.1080/17470910802253836.
Vannuscorps, G., Caramazza, A., 2016. Typical action perception and interpretation without motor simulation. Proc. Natl. Acad. Sci. U.S.A. 113, 86–91.
Van Overwalle, F., 2009. Social cognition and the brain: a meta-analysis. Hum. Brain Mapp. 30 (3), 829–858. https://doi.org/10.1002/hbm.20547.
Vogeley, K., 2017. Two social brains: neural mechanisms of intersubjectivity. Philos. Trans. R. Soc. Biol. Sci. 372, 20160245. https://doi.org/10.1098/rstb.2016.0245.
Vogeley, K., Bente, G., 2010. 'Artificial humans': psychology and neuroscience perspectives on embodiment and nonverbal communication. Neural Netw. 23, 1077–1090. https://doi.org/10.1016/j.neunet.2010.06.003.
Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happé, F., Falkai, P., Fink, G.R., Zilles, K., 2001. Mind reading: neural mechanisms of theory of mind and self-perspective. Neuroimage 14, 170–181. https://doi.org/10.1006/nimg.2001.0789.
Völlm, B.A., Taylor, A.N.W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J.F.W., Elliott, R., 2006. Neuronal correlates of theory of mind and empathy: a functional magnetic resonance imaging study in a nonverbal task. Neuroimage 29, 90–98. https://doi.org/10.1016/j.neuroimage.2005.07.022.
Wheatley, T., Milleville, S.C., Martin, A., 2007. Understanding animate agents: distinct roles for the social network and mirror system. Psychol. Sci. 18, 469–474. https://doi.org/10.1111/j.1467-9280.2007.01923.x.