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Understanding Body Language Does Not Require Matching the Body's Egocentric Map to Body Posture: A Brain Activation fMRI Study

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Abstract

Body language (BL) is a type of nonverbal communication in which the body communicates the message. We contrasted participants' cognitive processing of body representations or meanings versus body positions. Participants ($N = 20$) were shown pictures depicting body postures and were instructed to focus on their meaning (BL) or on the position of a body part relative to the position of another part (body structural description [BSD]). We examined activation in brain areas related to the two types of body representation—body schema and BSD—as modulated by the two tasks. We presumed that if understanding BL triggers embodiment of body posture, a matching procedure between the egocentric map coding the position of one's body segments in space and time should occur. We found that BL (vs. BSD) differentially activated the angular gyrus bilaterally, the anterior middle temporal gyrus, the temporal pole, and the right superior temporal gyrus, the inferior frontal gyrus, the superior medial gyrus, and the left superior frontal gyrus. BSD (vs. BL) differentially activated the superior parietal lobule (Area 7A) bilaterally,

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the posterior inferior temporal gyrus, the middle frontal gyrus, and the left precentral gyrus. Sensorimotor areas were differentially activated by BSD when compared with BL. Inclusive masking showed significant voxels in the superior colliculus and pulvinar, fusiform gyrus, inferior temporal gyrus, superior temporal gyrus, the intraparietal sulcus bilaterally, inferior frontal gyrus bilaterally, and precentral gyrus. These results indicate common brain networks for processing BL and BSD, for which some areas show differentially stronger or weaker processing of one task or the other, with the precuneus and the superior parietal lobule, the intraparietal sulcus, and sensorimotor areas most related to the BSD as activated by the BSD task. In contrast, the parietal operculum, an area related to the body schema, a representation crucial during embodiment of body postures, was not activated for implicit masking or for the differential contrasts.

Keywords
body language, functional magnetic resonance imaging, social neuroscience, sensorimotor cortex, modulation, rehabilitation

Introduction

Body language (BL) is a type of nonverbal communication, the so-called silent language (Hall, 1959). Whole body posture conveys affect-specific information (Atkinson, Dittrich, Gemmell, & Young, 2004). Accordingly, reading and processing body signals based on the meaningful position of body parts enable us to detect others' intentions, internal states, and motivations (e.g., Slaughter, Stone, & Reed, 2004), as the body conveys the message. This is a highly relevant communication skill, especially in clinical populations in which verbal language is impaired owing to a brain lesion, meaning that this ability can also play a role in neurorehabilitation.

It has been suggested that processing body posture information is partly an abstract ability and so involves more than just visual perception (Tipper, Signorini, & Grafton, 2015). Therefore, it is not surprising that BL processing triggers several areas of brain activation (de Gelder, 2006). Suggested neural correlates of BL processing (e.g., de Gelder, 2006) seem to involve three interconnected brain networks: (a) one for reflex-like emotional BL, (b) one for the visuomotor perception of BL, and (c) another for body awareness of BL. The first and the second networks are considered the two input systems (de Gelder, 2006), and they are interconnected with the third network related to one's own embodied awareness of perceived emotional states (Adolphs, Damasio, Tranel, Cooper, & Damasio, 2000; Damasio et al., 2000).

Each of these three cortical networks processes different types of body-related information (for more detail, see also Tipper et al., 2015). The rapid *automatic* perception of affective body expressions (occurring quickly and often unconsciously) involves the reflex-like emotional BL network that prepares adaptive reflexes and autonomic responses to emotionally provocative stimuli (e.g., fear inducing stimuli). This network mainly involves the pulvinar, superior colliculus, amygdala, and striatum. The second, visuomotor perception, network subserves decoding body meaning and involves the lateral occipital complex, superior temporal sulcus, intraparietal lobule, fusiform gyrus, amygdala, and premotor cortex. The visuomotor perception network includes areas related to the *visual* representation of the body, especially the extrastriate and fusiform gyrus/fusiform body areas triggered by the presentation of body forms and faces (Downing, Jiang, Shuman, & Kanwisher, 2001; Downing & Peelen, 2011); because a body posture implicitly implies a movement, body postures also activate the superior temporal sulcus, a motion-related area (Allison, Puce, & McCarthy, 2000). The brain's visual representation of BL is then translated into a *motor or proprioceptive* body representation.

Body posture activates the action observation network (e.g., de Gelder, 2006; de Gelder, De Borst, & Watson, 2015; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Grezes & Decety, 2001; Hari et al., 1998; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). The role of the action observation network in BL processing seems to be related to action understanding, through embodiment that is the simulation of one's own motor programs for an observed action. In the reported neuroanatomical model of BL processing, there is no mention of two other body representations in the human brain. One is the egocentric map coding the position of body segments in space and time, called *body schema* (Head & Holmes, 1911); the second is *body structural description* (BSD), an allocentric representation of the body that codes the position of each body segment relative to a standard body. Evidence for the egocentric map of the body can be found in the paradigm that requires participants to decide whether a hand presented in different orientation is a left or a right hand (Parsons, 1987a, 1987b, 1994; Parsons et al., 1995). Parsons argued that to carry out this task, participants mentally rotate a representation of their own body part until it aligns with the stimulus. The time required to complete the mental rotation of the body part, similar to the mental rotation of external visual objects, is an approximately linear function of the size of the angle required to superimpose the virtual to the presented image. The imagined trajectory for the observer's body part is strongly influenced by biomechanical constraints specific to its actual movement. Consistent with this position, Parsons (1994) argued on the basis of imaging data that motor imagery is involved in making implicit transformations of the viewer's hands and that the operation recruits motor processes. By contrast, evidence for the allocentric map of the body can be found in autotopagnosic patients who have a damaged visuospatial map that computes the spatial arrangement among parts of a standard body, the so-called BSD (Buxbaum & Coslett, 2001; Schwoebel & Coslett, 2005). The correlate of autotopagnosia has been identified in the left posterior parietal cortex (e.g., Schwoebel, Coslett, & Buxbaum, 2001). In a functional magnetic resonance imaging (fMRI) study, Felician et al. (2004) presented participants with a task similar to the one used to diagnose autotopagnosia and found an activation in both the left intraparietal sulcus (IPS) and the left superior parietal lobule (SPL). Lastly, in another fMRI study, Corradi, Hesse, Rumiati, and Fink (2008) presented two body parts (or buildings as control) and asked participants to evaluate their distance (or identified them as control) and found an activation of left posterior IPS when the distance between body parts was evaluated.

Taken together, studies indicate that the neural correlates of these two maps are the somatosensory cortex and the posterior IPS, respectively (e.g., Corradi-Dell'Acqua, Tomasino, & Fink, 2009). These two areas are included in the visuomotor perception network. Indeed, it has been shown that the parietal lobe is involved in the perception of the body and body movements (e.g., Allison et al., 2000). The egocentric and allocentric maps of the body become relevant in the BL network as, according to the embodied simulation theories, while processing a BL posture, we simulate and understand others' states by embodying their behavior (e.g., Gallese & Sinigaglia, 2011). Accordingly, embodying a posture implies matching the egocentric map coding the position of one's own body schema (Head & Holmes, 1911) with the position of the observed BL posture. In a previous study (Corradi-Dell'Acqua et al., 2009), we found that when participants assessed the handedness of a pictured arm by comparing it with their own (a body schema task), they activated the left secondary somatosensory cortex; on a control task in which they were asked to assess the handedness of an arm by comparing it with a simultaneously presented body map corresponding to an allocentric map of the body (a BSD task), they activated the left SPC, extending to the posterior IPS.

Embodiment is also mentioned with respect to the third, body awareness, BL network. The third network includes the parietal cortex (somatosensory), ventromedial prefrontal areas, and insula (Allison et al., 2000; de Gelder, 2006; Kana & Travers, 2012), and it is supposed to be related to one's own embodied awareness of perceived emotional states (Adolphs et al., 2000; Damasio et al., 2000). Adolphs et al. (2000) reported that a lesion in the right supramarginal gyrus (SMG) and the secondary somatosensory areas was associated with impaired abstract judgments for face stimuli. These authors explicitly referred to mental imagery in saying that their task might have implicitly triggered an online somatosensory representation by internal simulation.

In the current fMRI study, we further addressed the different networks involved in BL processing. We presented the same stimuli, depicting BL postures, in two different conditions: BL and BSD tasks. Participants, according to task instructions, had to attend to the meaning conveyed by body postures in the BL task and to the relative positioning of body parts relative to another body in the BSD task. The two tasks differed as to the body functional representation activated by task instructions. We hypothesized that these body representations (body schema and BSD) might be the same functional representation for the interaction between processing a body posture meaning and body posture position. Accordingly, by using the same stimuli, if reading BL (BL task) triggers embodiment, we should find the activated sensorimotor brain areas related to the egocentric map coding the position of one's own body segments in space and time (body schema). By contrast, in the control task (BSD) that did not require processing BL but merely processing body positioning relative to another body, we should find the activated brain areas related to the allocentric map of the body, coding the location of body parts relative to a standard body.

The two tasks trigger two cognitive processes that may appear different in many conditions: BL may require more global stimulus processing, while BSD may require a more specific (local) processing of the body part targeted by its accompanying phrase. However, extraction and comprehension of BL is based on a more specific (local) processing of the targeted body part as well. Second, the BL task may appear, for some stimuli, to have an additional emotional component that is not present in the BSD task. However, the potential strength of the experiment consisted in presenting the same stimulus set in both the BL and BSD tasks, meaning that any emotional component was equally present in the stimuli presented in both conditions, though irrelevant to completing the BSD task. It is the task instruction that drives the participant's attention to BL or BSD. In addition, most stimuli presented did not involve an emotional component (e.g., gestures such as pointing convey meaning without emotion).

Method

Participants

The study was advertised for staff and students of the Faculty of Medicine of Udine University. This recruitment strategy resulted in 30 volunteers. Of this initial number, 10 participants were found to be ineligible (six showed MRI incompatibility due to either metal implants or claustrophobia). Twenty (nine males, 11 females) right-handed (Edinburgh Inventory test; Oldfield, 1971) healthy participants (age range 20–54 years, M age = 31.3, SD = 9.71 years) explicitly gave informed consent to participate in the study. All were monolingual native speakers of Italian and had comparable levels of education (M = 15.55, SD = 2.18 years). Exclusion criteria were magnetic resonance incompatibility (metal implants, claustrophobia, etc.), history of neurological or psychiatric diseases (based on their responses on self-report measures), and use of prescription drugs. The study was approved by the local Ethics Committee and performed in accordance with the 2013 Fortaleza version of the Helsinki Declaration and subsequent amendments.

fMRI Task and Experimental Paradigm

Stimuli. Stimuli used in the fMRI task were derived from a previously conducted stimulus-norming study (see later). Line drawings were taken from illustrations by Piero and John Hepworth included in Pease and Pease (2004)'s *The Definitive Book of Body Language*. All the pictures depicted people showing attitudes and BL postures. The final set of stimuli that consisted of 44 pictures and their descriptions is provided in Table 1, along with a description of their meanings.

Stimulus norming study. The stimulus norming study included a second set of 20 healthy Italian, right-handed participants (nine males, 11 females; *M* age = 23.09, *SD* = 2.19 years, range 21–31*;* *M* education = 16.63, *SD* = 0.89 years, range 16–18), different than those participating to the fMRI study. All participants had normal or corrected-to-normal vision and no history of neurological illness, psychiatric disease, or drug abuse. Stimuli (*N* = 77) were singly presented on white sheets. The panel included five questions next to each picture: (a) Does the posture convey a meaning? (b) Which of these emotions could express the subject in the picture: surprise, anger, disgust, fear, happiness, sadness, or neutral? (c) On a 1-10 Likert scale, how strongly is this emotion represented? (d) Was it easy or difficult for you to recognize this emotion? (e) What does it mean? (The subject had to write a word or short sentence describing the meaning.) The test was presented in a comfortable and quiet environment. A typical testing session lasted around 40 minutes. We excluded data from two participants because they had not answered Question 1 in more than 80% of the pictures. The two exclusion criteria for the stimuli were (a) pictures that were not identified by more than five out of 18 participants or that were described as difficult to recognize (resulting in the exclusion of 33 pictures) and (b) high interrater agreement for each scale (see Table 2).

Tasks and Design

BL and BSD fMRI tasks. We presented 44 stimuli (311 × 317 Pixels) in the center of a computer screen on a white background, and one additional stimulus (n#3) was repeated twice (once in each of the two tasks). We presented 18 blocks (15 seconds each) of both the BL task (*N* = 9) and the BSD task (*N* = 9), interspersing them with a 12-second fixation baseline rest period. Before each block, participants viewed a 3-second instruction informing them about the upcoming task. Each block included five stimuli (3 seconds each) randomized with no repetition (except for stimulus item n#3 that was repeated twice in the last block of both the BL and BSD tasks, respectively). The block order (i.e., BL or BSD) was randomized, and the task lasted 9 for minutes.

Two verbal expressions were shown in the lower left and right sides of the screen, below each picture. The verbal labels for each stimulus are shown in

Table 1. Stimulus List: Description of Posture, Page, and Meaning as Reported in *The Definitive Book of Body Language* (Allan and Barbara Pease) Published by Pease International.

	Posture description	Picture on page	Meaning according to the book	BL alternative labels		BSD alternative labels	
1	Shoulder shrug	20	Person does not know or does not understand what you are saying	impossibility	annoyance	open arms	arms along the hips
2	Critical evaluation gesture	22	Listener is having critical thoughts about what he hears	thoughtful	grateful	index on the cheek	hand on the thigh
3	Arms and legs tightly crossed and chin down	24	Defensive	wait	closure	hanging arms	crossed arms
4	Child telling a lie; she has wide eyes	25	Telling a lie	scared	closure	hands on the nose	hands on the mouth
5	Hold both palms out to the other person	33	Openness	openness	embarrassment	wide open arms	arms up
6	The power player	47	Attempts to control the other person	I am sorry	calm down	hands in midair	hands in pocket
7	Double-hander	54	Tries to give the impression he is trustworthy and honest	will you marry me?	congratulations	folded hands	handshake
8	Crossed arms on chest	93	Defensive or negative meaning	boredom	anger	arms along the hips	crossed arms
9	Fists clenched-arms crossed	96	Shows a hostile attitude/ defensiveness	boredom	interest	serious look	sharp-eyed
10	The double arm grip	96	Feeling insecure	worried	scared	crossed arms	arms behind the back
11	Handbag used to form a barrier	102	Allows the insecure person to form an almost unnoticeable arm barrier	why do you look at me?	scare	hands along the hips	hands holding handbag

(continued)

Table 1. Continued.

	Posture description	Picture on page	Meaning according to the book	BL alternative labels		BSD alternative labels	
12	The arm barrier says "no"	103	Someone who is feeling hesitant, unsure, or negative about what they are hearing	sadness	dismay	arms on the table	arms up
13	Rubbing the palms together	129	Showing positive expectancy	happiness	exhilaration	folded hands	clenching fists
14	Rubbing the palms together	130	Signals that he is expecting to see something good and might buy	diabolic	envying	smoothed brow	furrowed brow
15	Rubbing the thumb against the index finger or fingertips	130	Money expectancy gesture. "We can make money out of this!"	pay attention	how much does it cost	fingertips together	crossed fingers
16	Steepling	133	Confident he has the right answers	superiority	pensive	open mouth	smiling
17	The face platter	135	Presenting her face for a man to admire	concern/interest	happiness	hand on the cheek	hand above the chin
18	Arms folded with thumbs pointing upward	141	Feeling superior	annoyance	disgust	smoothed brow	furrowed brow
19	The mouth cover	148	To suppress the deceitful words that are being said	disinterest	hesitation	the hand supporting the face	hands along the hip
20	The "Shhh" gesture, where one finger is placed vertically over the lips	149	An attempt to tell themselves not to say something	give me some time	silent please	index on the mouth	index on the nose
21	The collar pull	153	When they lie and suspect they have been caught out when the deceiver feels that you suspect he is not telling the truth	superiority	pensive	hand pulling the collar	wrenching the neck

(continued)

Table 1. Continued.

	Posture description	Picture on page	Meaning according to the book	BL alternative labels		BSD alternative labels	
22	The hand supporting the head	155	It is a signal that boredom has set in, and his supporting hand is an attempt to hold his head up to stop himself from falling asleep	satisfied	bored	hand on the cheek	hand on the chin
23	Hand begins to support the head	156	Having negative thoughts	thoughtful	bored	good look	brooding look
24	Hand moved to the chin, and the hand may also be stroking the chin	160	Evaluation/decision-making cluster	anxious	thoughtful	elbow along the hip	elbow on the leg
25	"Pain in the neck" gesture	161	When you feel frustrated or fearful	thoughtful	romantic	hand on the forehead	hand on the back of the head
26	Slapping oneself	162	Punishing oneself	tired	careless	palm on the forehead	palm on the cheek
27	The eyebrow flash	171	Greeting signal	happiness	discomfort	closed mouth	half-open mouth
28	The standing leg cross	214	Shows a closed, submissive, or defensive attitude	wait	gratitude	stretched legs	crossed legs
29	The standing leg cross	216	She is more likely to be cold or just looking for the rest room, 216, nervous, anxious, or defensive	doubtful	closure	good look	steely gaze
30	Attention position arms and legs crossed	217	Uncertain about each other	conversation	dispute	eyes down	staring in the eyes
31	The standing leg open	217	Openness and acceptance	enthusiasm	openness	hanging arms	arms along the hips
32	Head down	235	Shows disapproval or dejection	temptation	challenge	close mouth	open mouth
33	The head duck	236	Trying to appear smaller not to cause offence to others	shy	challenge	shrugging of shoulders	shoulders relaxed

(continued)

Table 1. Continued.

	Posture description	Picture on page	Meaning according to the book	BL alternative labels		BSD alternative labels	
34	Hands on hips	239	Used by models to make clothing more appealing	vanity	subordination	hands along the hips	hands on the hips
35	Hands-on-hips gesture	241	Gesture clusters show aggressive attitudes	annoyed	indignant	hands along the hips	hand on the belt
36	Leg over the arm of chair	243	Has an informal, aggressive attitude	relaxed	charming	elevated left leg	stretched left leg
37	Straddling a chair	244	The straddler wants to dominate or control while, at the same time, protecting his front	aversion	wait	stretched arms	crossed arms
38	Seated version of the hands-on-hips pose except that hands are behind the head with the elbows menacingly pointed out	245	It is almost entirely a male gesture used to intimidate others or it infers a relaxed attitude to lull you into a false sense of security just before he ambushes you	distraction	comfort	hand on the face	hands on the back of the head
39	Placing one arm of the frame of the glasses in the mouth	272	Using the glasses to stall for time	provocation	concentration	frame of the glasses in the mouth	frame of the glasses in the hand
40	Peering over the glasses	272	Intimidates everyone	inspect	get angry	close eyes	open eyes
41	Seated body pointing	284	Body pointing is used to close off a couple and exclude another man on the right	closure	openness	crossed arms	arms along the hips
42	Connecting the item (a car) to their body	318	Showing ownership	proudness	tranquility	left leg on the floor	left leg on the car

(continued)

Table 1. Continued.

	Posture description	Picture on page	Meaning according to the book	BL alternative labels		BSD alternative labels	
43	The doorway intimidator, an upright stance with palms visible	319	To create a favorable impression on other	self-confidence	wait	arm on the wall	arm on the hip
44	Claiming ownership of the desk placing his foot hard against the of the desk	320	To stake his claim to it	indifference	comfort	feet on the table	feet on the floor

Note. BL and BSD were used as alternative labels. Correct answers are given in gray. BL = body language; BSD = body structural description.

Table 2. Interrater Agreements for Characteristics of Specific Body Language Pictures.

Scale	*M* (*SD*) rating	Overall Cronbach's alpha	Cronbach's alpha if each corresponding item was deleted to identify weaker or stronger items
Meaningfulness	0.88 (0.098)	.875	>.8 for each item
Emotion attribution	2 items were judged as anger, 7 as disgust, 13 as fear, 14 as happiness, 8 as sadness, and none as neutral	.960	>.8 for each item
Strength	6.01 (0.86)	.983	>.9 for each item
Difficulty	0.84 (0.08)	.85	>.8 for each item

Table 1. The same stimuli appeared twice, once in the BL and once in the BSD task. Participants had to choose one of two verbal labels that best described the picture according to the task instructions. In the BL task, the following instruction was given: "Pay attention to body language: choose one of the two expressions below the picture that is more closely associated with the image by pressing the corresponding button (left or right)." Verbal expressions explained BL-related concepts or adjectives (e.g., self-confidence). With regard to choosing the verbal labels associated with the picture, we selected the expression showing the closest interparticipant agreement during the preliminary stimulus norming study described earlier (e.g., if 80% of participants described Picture 1 as "self-confidence," we used this descriptor as the correct verbal expression to pair with this picture). Table 1 shows the meaning of the posture as found in *The Definitive Book of Body Language*, from which the pictures were taken. As alternative labels, we selected the label used by the lowest number of participants (maximum of 1–2 participants) during the stimulus norming study to describe the same picture. The BSD task instruction was as follows: "Pay attention to the position of body parts: choose one of the two expressions below the picture that is more closely associated with the image by pressing the corresponding button (left or right)." Verbal expressions described the position of a specific body part represented in the picture (e.g., hands on mouth). For the verbal label, we used a visual description, based on the BSD of the picture (e.g., hands on mouth). We created the alternative label using the same body part with another body target (e.g., hands on nose).

fMRI Data Acquisition

In the fMRI scanner, participants laid supine with their head fixated by firm foam pads. Stimuli (“Presentation,” Neurobehavioral Systems Inc., CA, USA) were projected through a VisuaStim Goggles system (Resonance Technology, Northridge, USA), and participants were asked to answer by pressing two keys on an MRI-compatible response device (Lumitouch, Lightwave Medical Industries, Coldswitch Technologies, Richmond, CA, USA) with their right or left index finger. Prior to the experiment, participants practiced the task outside the scanner ($N = 10$ trials).

A 3-T Philips Achieva whole-body scanner was used to acquire T1-weighted anatomical images and functional images using a SENSE Head 8-channel head coil and a custom-built head restrainer to minimize head movements. Functional images were obtained using a T2*-weighted EPI sequence of the whole brain. EPI volumes ($n = 182$) contained 32 transverse axial slices (repetition time = 3,000 milliseconds, echo time = 35 milliseconds, field of view = 23 cm, acquisition matrix = 128×128, slice thickness = 3 mm with no gaps, flip angle = 90°, voxel size = $1.8 \times 1.8 \times 3$ mm) and were preceded by five dummy images that allowed the scanner to reach a steady state. After functional neuroimaging, high-resolution anatomical images were acquired using a T1-weighted 3-D magnetization-prepared, rapid acquisition gradient fast field echo (T1W 3D TFE SENSE) pulse sequence (repetition time = 8.2 milliseconds, echo time = 3.76 milliseconds, field of view = 24 cm, 190 transverse axial slices of 1 mm thickness, flip angle = 8°, voxel size = $1 \times 1 \times 1$ mm) lasting for 8.8 minutes.

Data Analysis

fMRI data processing. The fMRI data preprocessing and statistical analyses were performed on a UNIX workstation (Ubuntu 8.04 LTS, i386, www.ubuntu.com/) using MATLAB r2007b (The Mathworks, Inc., Natick, MA, USA) and SPM8 (Statistical Parametric Mapping software, SPM; Wellcome Department of Imaging Neuroscience, London, UK, www.fil.ion.ucl.ac.uk/spm). After discarding the first five dummy volumes to allow for T1 equilibration effects, we spatially realigned the images to the reference volume (i.e., the now first/previously seventh acquired volume). T1 anatomical images were coregistered to the mean EPI image and normalized to the standard SPMT1 single-subject template in MNI space. A Gaussian kernel of 8-mm full-width half-maximum was used for smoothing to meet the statistical requirements of the theory of Gaussian fields according to the General Linear Model employed in SPM and to compensate for interindividual variability in macro- and microanatomical structures across participants (Friston et al., 1995a, 1995c). To delineate the network involved in each task, a general linear model for blocked designs was applied to each voxel of the functional data by modeling the activation and the baseline conditions for each participant and their temporal derivatives by means of reference waveforms that correspond to boxcar functions convolved with a hemodynamic response function (Friston et al., 1995c; Friston, Frith, Turner, & Frackowiak, 1995b). The presentation of the BL and BSD tasks and the baseline condition were modeled as regressors of main interest. Furthermore, for each analysis, we included six additional regressors that modeled the head movement parameters obtained from the realignment procedure as covariates of no interest. Low-frequency signal drifts were filtered using a cutoff period of 1/128 Hz. At the single participant level, specific effects were assessed by applying appropriate linear contrasts to the parameter estimates of the experimental conditions resulting in t statistics for each voxel.

These t statistics were then Z transformed to statistical parametric maps (SPM$\{Z\}$) of differences between experimental conditions and between experimental conditions and baseline. SPM$\{Z\}$ statistics were interpreted in light of the probabilistic behavior theory of Gaussian random fields (Friston et al., 1995b, 1995c). For each participant, we calculated the following contrast images: BL–BSD and BSD–BL and BL–baseline and BSD–baseline. For the second-level random effects analysis, contrast images obtained from individual participants were entered into a one-sample t test to create an SPM$\{\mathrm{T}\}$ indicative of significant activations specific for this contrast on a group level. We used a threshold of $p < .05$, corrected for multiple comparisons at the cluster level (Familywise Error [FWE] correction), with a height threshold at the voxel level of $p < .001$, uncorrected. The anatomical interpretation of functional imaging results was performed using the SPM Anatomy toolbox (Eickhoff et al., 2005).

Behavioral data. We checked for normal distribution of the participants' choices and reaction times (RTs) by Shapiro–Wilk testing. We performed a repeated-measure analysis of variance with tasks (BL, BSD) as factors on the participants' mean RTs. We performed a Wilcoxon signed rank-test on the participants' mean choices. Because we used an associative task, that is, matching verbal label and picture, we could not calculate accuracy data. We calculated the percentage of participants' choices corresponding to the most closely associated answers (i.e., the expression showing the closer intersubject agreement during the stimulus norming study). Analyses were performed by SPSS for Windows (version 12.0).

Results

Neural Activations

Main effect of TASK: BL versus BSD (and vice versa). The contrast images (threshold of $p < .05$, corrected for multiple comparisons at the cluster level [FWE correction], with a height threshold at the voxel level of $p < .001$, uncorrected) for BL task > baseline and for BSD > *baseline* were almost the same (see Table 3 and Supplemental Figure 1), whereas the areas recruited by BL > BSD

Table 3. Whole Brain Analysis: Brain Regions Showing Significant Relative Increases in BOLD Responses Associated With Body Language (BL) and Body Structural Description (BSD) Tasks.

		MNI				Cluster size
Region	Side	*x*	*y*	*z*	*Z*	(voxel)
BL–BSD						
Middle occipital gyrus	LH	−12	−102	4	4.82	29
Angular gyrus	RH	56	−64	30	4.57	63
Angular gyrus	LH	−50	−64	34	4.41	64
Anterior superior temporal sulcus	LH	−54	−10	−20	4.41	125
Anterior superior temporal sulcus	RH	56	−4	−20	4.88	205
Temporal pole	RH	44	14	−24	4.85	
Temporal pole	LH	−42	12	−26	4.83	81
Superior temporal gyrus	RH	46	−24	−4	4.46	26
Inferior frontal gyrus (pars orbitalis)	LH	−46	20	−12	4.37	153
Inferior frontal gyrus (pars triangularis)	LH	−50	24	2	4.32	
Inferior frontal gyrus (pars triangularis)	RH	52	30	14	5.03	97
Superior medial frontal gyrus	LH	−4	56	32	4.30	88
Superior medial frontal gyrus	RH	0	60	4	4.21	56
Superior frontal gyrus	LH	−16	40	44	3.96	29
BSD–BL						
Calcarine gyrus	RH	12	−80	6	6.03	11,674
Superior parietal lobule (Area 7)	RH	12	−79	49	5.71	
Lingual gyrus	LH	−16	−58	0	6.01	
Superior parietal lobule (Area 7)	LH	−8	−72	57	6.01	
Middle cingulate cortex	M	4	−28	46	4.28	48
Middle occipital gyrus	LH	−40	−80	16	3.96	55
Middle temporal gyrus	LH	−48	−72	14	3.28	
Inferior temporal gyrus	RH	56	−54	−12	4.37	80
Inferior temporal gyrus	LH	−54	−64	−6	4.47	130
Precentral gyrus	LH	−40	0	34	4.94	291
Inferior frontal gyrus (pars opercularis)	LH	−46	4	26	4.43	
Supplementary motor area	M	0	6	52	4.70	45
Superior frontal gyrus	RH	28	4	58	4.90	153
Middle frontal gyrus	RH	38	32	38	4.69	263
Middle frontal gyrus	LH	−28	0	54	4.59	278
Middle frontal gyrus	RH	36	44	2	4.10	31

(continued)

Table 3. Continued.

Region	Side	MNI x	MNI y	MNI z	Z	Cluster size (voxel)
Middle frontal gyrus	RH	26	52	−2	3.56	33
BL-rest						
Inferior temporal gyrus	RH	46	−72	−10	7.00	20,932
Thalamus	LH	−16	−30	−2	6.40	1,390
Precentral gyrus	LH	−40	2	34	5.73	4,689
Temporal pole	LH	−50	14	−16	5.65	
Inferior frontal gyrus (pars triangularis)	LH	−52	16	24	5.64	
Postcentral gyrus (Area 2)	RH	46	−28	54	4.70	269
Precentral gyrus (Area 4a)		38	−32	56		
BSD-rest						
Inferior temporal gyrus	RH	46	−52	−18	6.96	20,820
Insula lobe	RH	32	26	−2	6.47	4,171
Supplementary motor area		−6	16	44	5.98	
Middle frontal gyrus		38	0	60	5.89	
Thalamus	LH	−4	−22	−2	5.78	1,022
Inferior frontal gyrus (pars triangularis)	LH	−52	16	26	6.12	3,744
Insula lobe		−32	22	0	6.11	
Precentral gyrus		−40	2	34	6.00	
Caudate nucleus	RH	16	6	14	5.51	576
Thalamus		16	−22	12	5.28	
Putamen	LH	−22	−2	8	5.62	479
Thalamus		−14	−14	12	5.22	
Caudate nucleus		−12	−6	16	5.10	
BL-rest masked (inclusive) by BSD-rest						
Inferior temporal gyrus	RH	46	−72	−10	7.00	15,953
Fusiform gyrus		42	−58	−16	6.86	
Thalamus	LH	−16	−30	−2	6.40	1,369
Supplementary motor area	M	−4	18	44	6.04	4,645
Inferior frontal gyrus (pars triangularis)	RH	30	26	−2	5.63	
Precentral gyrus	LH	−40	2	34	5.73	4,481
Temporal pole		−50	14	−16	5.65	
Inferior frontal gyrus (pars triangularis)		−52	16	24	5.64	
Postcentral gyrus (Areas 2, 3b)	RH	46	−28	54	4.70	142
Precentral gyrus (Area 4a)	RH	38	−20	50	3.96	118

(continued)

Table 3. Continued.

Region	Side	MNI *x*	MNI *y*	MNI *z*	*Z*	Cluster size (voxel)
BL-rest masked (exclusive) by BSD-rest						
Temporal pole	RH	46	16	−24	7.98	106
Inferior frontal gyrus (pars triangularis)	RH	54	28	−2	6.89	58
Inferior frontal gyrus (pars orbitalis)		44	34	−4	4.79	
Superior temporal gyrus	RH	54	−10	−14	6.59	37
Middle temporal gyrus		56	0	−22	4.99	
Temporal pole	LH	−44	18	−22	6.32	114
Inferior frontal gyrus (pars orbitalis)		−38	24	−12	5.87	
Inferior frontal gyrus (pars triangularis)	RH	52	24	14	6.14	38
Middle temporal gyrus	LH	−60	−6	−14	5.79	56
Temporal pole		−52	6	−18	5.60	
BSD-rest masked (exclusive) by BL-rest						
Superior parietal lobule	LH	−14	−68	44	5.17	145
Precuneus		−10	−76	48	4.84	
Precuneus	RH	16	−74	48	4.73	130
Supramarginal gyrus	LH	−58	−26	40	4.63	128
Inferior parietal lobule		−58	−36	40	4.48	
Inferior parietal lobule	RH	42	−44	40	4.42	124
Supramarginal gyrus		40	−54	42	4.13	
Middle frontal gyrus	LH	−20	6	50	3.95	43
BSD–BL[a]						
Inferior parietal lobule (Area 2)	LH	−42	−38	44	5.01	35
Inferior parietal lobule (Area 2)	RH	38	−38	38	4.86	49
Inferior parietal lobule (Area 2, 1)	LH	−42	−44	58	4.12	27
Inferior parietal lobule (Area 2)	RH	38	−44	58	3.69	16
Inferior parietal lobule (Area 2, 1)	LH	−30	−48	54	3.48	17
BL–BSD[a]						
–	–	–	–	–	–	–

Note. For each region of activation, the coordinates in MNI space are provided in reference to the maximally activated voxel within an area of activation, as indicated by the highest *Z* value ($p < .05$, corrected for multiple comparisons at the cluster level, height threshold $p < .001$, uncorrected). LH/RH = left/right, M = medial, MNI = Montreal Neurological Institute.

[a] Region of interest (ROI) analysis.

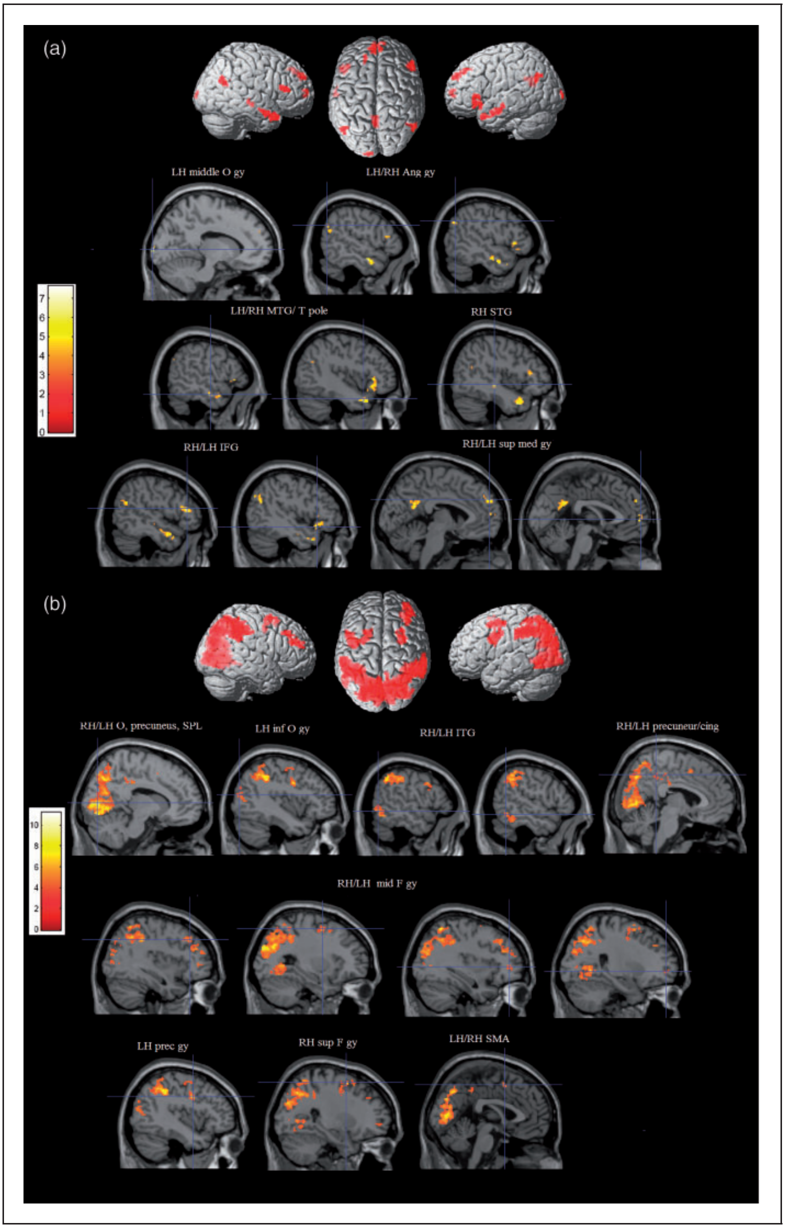

Figure 1. Areas of differential activation related to the BL task relative to BSD and the BSD task relative to BL. Activations were superimposed on a lateral surface of a 3-D surface rendering and on an axial coronal and sagittal slice of the spatially normalized single-subject template brain provided by SPM8.

LH/RH = left/right; MTG = middle temporal gyrus; STG = superior temporal gyrus; IFG = inferior frontal gyrus; ITG = inferior temporal gyrus; SPL = superior parietal lobule; SMA = supplementary motor area.

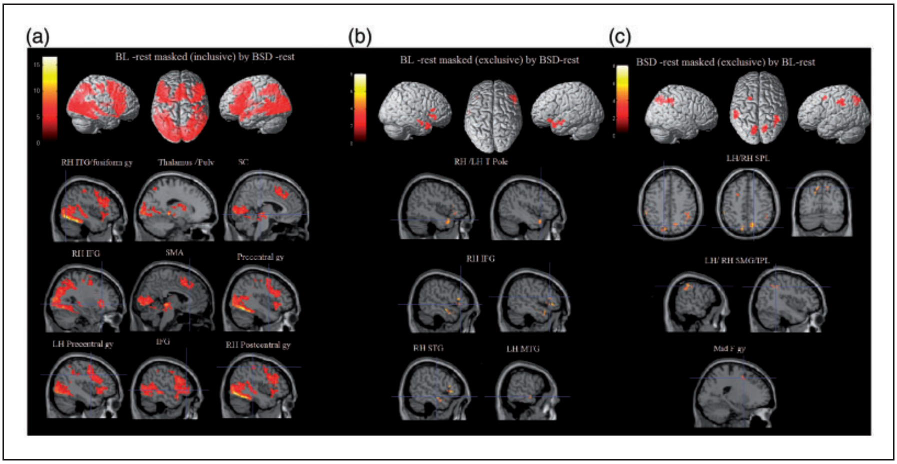

Figure 2. Areas of activation related to BL-rest masked (inclusive) by BSD-rest (a), BL-rest masked (exclusive) by BSD-rest (b), and BSD-rest masked (exclusive) by BL-rest (c). Activations were superimposed on a lateral surface of a 3-D surface rendering and on an axial coronal and sagittal slice of the spatially normalized single-subject template brain provided by SPM8.

BL = body language; BSD = body structural description; LH/RH = left/right; ITG = inferior temporal gyrus; SC = superior colliculus; IFG = inferior frontal gyrus; SMA = supplementary motor area; MTG = middle temporal gyrus; STG = superior temporal gyrus; SPL = superior parietal lobule; IPL = inferior parietal lobule; SMG = supramarginal gyrus.

(see Figure 1 and Table 3) were the (a) middle occipital gyrus (MOcG), (b) angular gyrus (AG), (c) anterior temporal sulcus, (d) temporal pole, (e) inferior frontal gyrus (IFG), (f) superior medial frontal gyrus, all bilaterally, and, in addition, the (g) right superior temporal gyrus (STG) and (h) left superior frontal gyrus (see Table 3).

The areas recruited for the BSD > BL (see Figure 1) involved the (a) calcarine gyrus, (b) left MOcG, (c) precuneus, (d) SPL and IPL, (e) inferior temporal gyrus (ITG), (f) medial precuneus, (g) middle cingulus, (h) SMA, (i) middle frontal gyrus (MFG) bilaterally, and (i) left precentral gyrus (PcG; Areas 6 and 4a) and the SMA extending to the left IFG (pars opercularis; see Table 3).

Inclusive and exclusive masking. We discarded activation related to the BSD by masking all voxels above the threshold $(p < .05$ corrected; exclusive masking) activated by the contrast of BSD versus the rest task (see Figure 2(c)). BL-rest masked (exclusive) by BSD-rest involved clusters of activity in the (a) right temporal pole, (b) right IFG, (c) right superior and middle temporal gyrus (MTG), (d) left temporal pole, extending to the IFG, and (e) left MTG. We discarded activation related to the BL by masking all voxels above the threshold

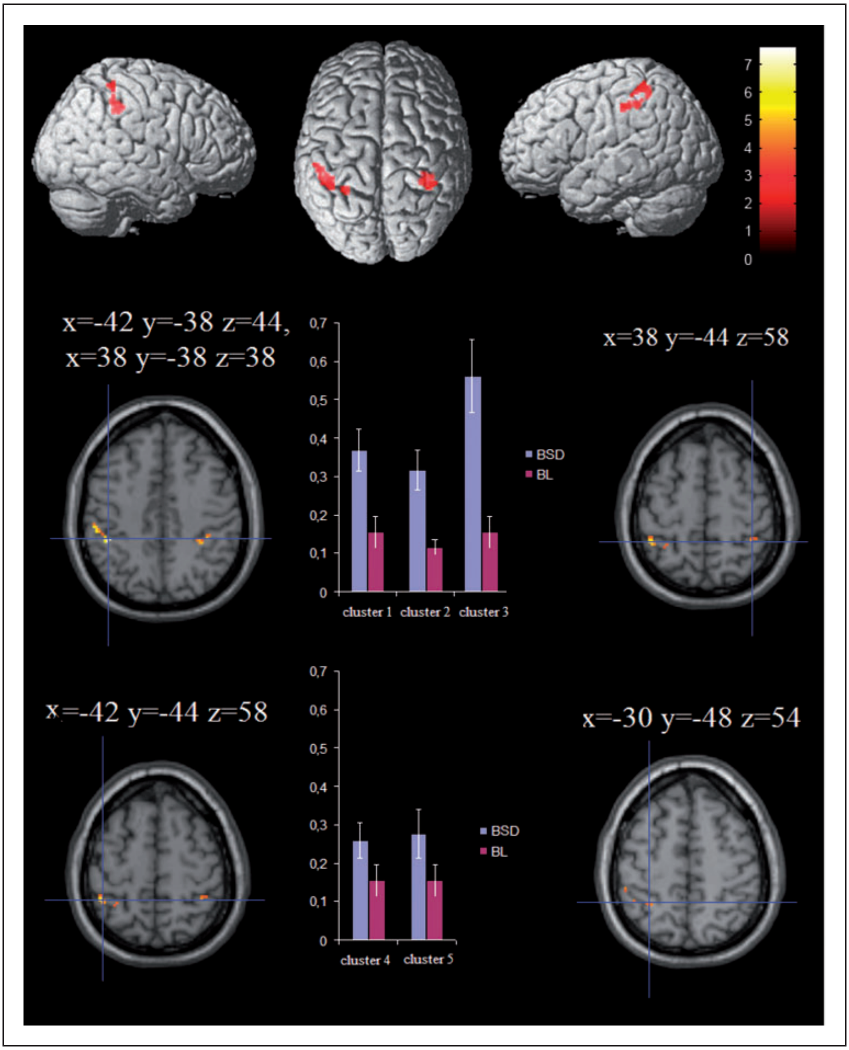

Figure 3. Region of interest (ROI) analysis showing that the sensorimotor cortex was differentially recruited by the BSD as compared with BL task. The same ROI analysis performed on the BL versus BSD contrast did not yield any significant activation. The activation clusters were superimposed on a lateral surface of a 3-D surface rendering (SPM8) and on an axial slice of the spatially normalized single-subject template brain provided by SPM8. Their respective plots of relative BOLD signal changes at the maximally activated voxel are shown. Mean and standard error are provided.

BL = body language; BSD = body structural description.

($p < .05$ corrected; exclusive masking) activated by the contrast of BL versus rest tasks (see Figure 2(b)).

BSD-rest masked (exclusive) by BL-rest involved clusters of activity in the (a) left SPL, extending to the precuneus, (b) right SPL, extending to the precuneus, (c) left IPL, extending to the SMG, (d) right IPL, extending to the SMG, and (e) left MFG.

To show voxels within the mask image, we used inclusive masking (see Figure 2(a)). BL-rest masked (inclusive) by BSD-rest involved clusters of activity in the (a) right ITG, extending to the left ITG, to the inferior and MOcG and to the IPL and SPL bilaterally, (b) thalamus bilaterally, (c) left PcG, extending to the IFG, (d) right IFG and the PcG, and (e) right pre- and postcentral gyrus.

ROI analysis on the sensorimotor cortex. To further address the role of sensorimotor areas in processing BSD and body communication, we performed an Region of interest (ROI) analysis using wfu_pickatlas and SPM8 (http://www.fil.ion.ucl.ac.uk/spm/ext/) on an anatomical mask created with the Anatomy toolbox (http://www.fz-juelich.de/inm/inm-1/DE/Forschung/_docs/SPMAnatomyToolbox/SPMAnatomyToolbox_node.html) comprising, in the same ROI, the probabilistic cytoarchitectonic maps of the primary somatosensory cortex (Areas 3a, 3b, 1, 2) and the motor cortex (Areas 4a and 4p) of the left and the right hemisphere (using a threshold of $p < .05$, FWE corrected at the voxel level). We found that BSD versus BL tasks differentially recruited the left and the right IPL (Areas 1 and 2; see Table 3 and Figure 3). The same ROI analysis performed on the BL versus BSD contrast did not yield any significant activation.

Behavioural Results

RTs were normally distributed given Shapiro–Wilk test results of $p = .88$ for the BL condition and $p = .57$ for the BSD condition. Participants' choices were not normally distributed, given results of $p = .48$ for the BL condition and $p = .009$ for the BSD condition.

RTs were significantly shorter, $F(1, 19) = 10.112$, $p < .005$, in the BL condition ($M = 1.77$, $SD = 0.21$ seconds) versus the BSD condition ($M = 1.87$, $SD = 0.14$ seconds). The percentage of participants' choices corresponding to the most closely associated answers (i.e., the verbal expression showing the closer interparticipant agreement during the stimulus norming study) was significantly higher ($Z = 3.73$, $p < .001$) for the BSD condition (93.66%) versus the BL condition (82.53%).

Discussion

In this fMRI study, we further investigated the nature of previously reported sensorimotor cortex involvement in BL processing (e.g., de Gelder, 2006; de Gelder et al., 2015). Before discussing our main finding of a differential enhancement of sensorimotor activity in the BSD-BL contrast, we will first discuss the differential brain activations associated with the BL and BSD tasks.

Differential Activation for the BL Task

The BL (relative to the BSD) activated the AG, the anterior STG/temporal pole, the right STG, the IFG, and the superior medial gyrus bilaterally. The AG is involved in processing and abstracting social /emotional meaning (for a recent quantitative meta-analysis of neuroimaging studies, see Bzdok et al., 2016). In our study, our finding of a BL bilateral activation of the AG can be related to the processing of meaningful gestures. The left AG is activated in processing meaningful actions (e.g., Rumiati et al., 2005), while the right AG could be related to the socioemotional nature of meaningful gestures. As to the *anterior* temporal sulcus, two other BL processing studies found this activation during BL processing (Centelles, Assaiante, Nazarian, Anton, & Schmitz, 2011; Sinke, Sorger, Goebel, & de Gelder, 2010). Consistent with our results, other studies also found temporal pole activation attributable to processing others' mental states (Brunet, Sarfati, Hardy-Bayle, & Decety, 2000; Castelli, Happe, Frith, & Frith, 2000; Gallagher et al., 2000).

BL activated the pars triangularis and pars orbitalis of the IFG, as in previous studies reporting IFG activation related to BL (e.g., Centelles et al., 2011; Kana & Travers, 2012; Libero, Stevens, & Kana, 2014; Prochnow et al., 2013; Sinke et al., 2010; Tipper et al., 2015). Lastly, ventromedial prefrontal cortex activation was also observed, as seen during theory of mind processing (Krause, Enticott, Zangen, & Fitzgerald, 2012) and during a task triggering empathic concern for another person's affective state (e.g., Shamay-Tsoory & Aharon-Peretz, 2007; Vollm et al., 2006).

Differential Activation Triggered by the BSD Task

The BSD task (relative to the BL task) activated the lateral occipital cortex/fusiform gyrus, the SPL, the precentral/IFG (pars opercularis), and the MFG. Activation of the occipital cortex/fusiform gyrus is consistent with the evidence that the lateral occipital cortex/fusiform gyrus is activated by the mere presentation of a body form (Downing et al., 2001, 2011) together with the fusiform gyrus/fusiform body area (Peelen & Downing, 2005, 2007) that code for the visual representation of the human body form. Activation of the SPL for BSD is in line with the role of this area in processing mental representations of the body image and of BSD (e.g., Corradi-Dell'Acqua et al., 2008, 2009). Lastly, the BSD task (vs. the BL task) activated the right dorsal parts of the prefrontal cortex, likely related to directing attention to a body portion, given the relation of this area to selective attention (Curtis & D'Esposito, 2003).

Possibly, it just takes more effort to analyze, rather than automatically process, the meaning, resulting in stronger sensorimotor (and other BSD task-related) activation. This argument is in line with the longer RTs for the BSD condition. In the language domain, it has been suggested that if a word is overlearned (e.g., it has been previously seen a sufficient number of times), then its presentation is processed through the direct, lexico-semantic route, and it may be globally recognized as a prelearned word form (e.g., Warrington & Shallice, 1980). Similarly, in the action recognition domain, the cognitive neuropsychological model of praxis (e.g., Cubelli, Marchetti, Boscolo, & Della Sala, 2000; Rothi, Ochipa, & Heilman, 1991) also includes a direct route (action input lexicon → action output lexicon). In the BL task, processing body postures might be so overlearned that it is not necessary to further analyze them for understanding.

We found differential activation in the superior and inferior parietal cortex, the left PcG (Areas 6 and 4a), and the SMA for the BSD, when compared with BL, task. In addition, an ROI analysis showed differential activation for BSD versus BL in the left and the right IPL (Areas 1 and 2). The role of sensorimotor activation in the processing of BL postures is far from clear. Prior studies showed that the sensorimotor cortex is activated independently of the (emotional) nature of the stimuli. For example, Borgomaneri, Gazzola, and Avenanti (2012) showed that performing TMS on the primary motor hand area while participants were observing and categorizing emotional and neutral International Affective Picture System stimuli led to increased motor excitability, when compared with watching landscapes or household objects. However, they showed that motor excitability was comparable for emotional and neutral body actions and argued that action simulation—corresponding to implicit taking of the body posture—may occur independently of whether the observed implied action expresses an emotional or neutral meaning.

Brain Areas Equally Shared by Both Tasks (Inclusive Mask) and Areas Used Uniquely by Either Task (Exclusive Mask)

The inclusive masking, showing significant voxels for BL-rest within the BSD-rest mask image, involved clusters of activity in part of the reflex-like brain processing regions (e.g., de Gelder, Snyder, Greve, Gerad, & Hadjikhani, 2004), namely, the superior colliculus and pulvinar, and part of the visuomotor processing regions (e.g., de Gelder et al., 2004), namely, fusiform gyrus, ITG, STG, the IPS bilaterally, IFG bilaterally, and PcG. The exclusive masking procedure confirmed part of the results of the BL versus BSD and BSD versus BL differential maps, namely, the temporal pole and IFG and ITG/MTG bilaterally for the BL task and the SPL and IPL and the precuneus and the MFG for the BSD task.

With respect to the activation in areas related to body representations (body schema and BSD) that might be the same functional representations involved by the BL and BSD tasks, we found that the precuneus and the SPL and IPS were associated with the exclusive masking procedure for BSD versus BL and were differentially activated by the BSD versus BL contrast. However, neither the masking nor the differential contrasts found activation in the parietal operculum (OP1; Eickhoff, Amunts, Mohlberg, & Zilles, 2006; Eickhoff, Schleicher, Zilles, & Amunts, 2006) corresponding to the secondary somatosensory cortex, the area that in our previous study (Corradi-Dell'Acqua et al., 2009) was activated when participants assessed the handedness of an arm picture by comparing it with their own (i.e., body schema task). This result is at variance with embodied simulation theories that argue that in processing a BL posture, we embody the posture (e.g., Gallese & Sinigaglia, 2011).

Limitations and Directions for Future Research

Among limitations of our study, the necessity of using small participant samples for multiple brain activation measurements in expensive fMRI research raises important questions about the broad generalizability of these findings for our populations. Second, we acknowledge that even though our BL and BSD tasks were based on the same stimuli, they may have sometimes differed in their requirements for global versus local image processing and in their involvement of single versus multiword word descriptions. Choosing an event-related design versus block design methodology may have allowed us to have added some parametric modulations/covariates or other refined analyses to the mode. Future studies should further address these concerns.

Conclusion

We found common networks for BL and BSD processing, with component parts that are differentially stronger or weaker in processing one task or the other. Brain areas related to the allocentric map of the body were activated by the BSD task, while those related to the body schema, an egocentric mental representation that is crucial during embodiment of body postures, was not activated by the BL task. From a rehabilitation research perspective, our results indicate that the network involved in BL is particularly complex, as BL is a type of abstract nonverbal communication. Our results are extremely relevant to rehabilitation as they show that training focused on processing body positions and postures activates sensorimotor areas.

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Supplemental material

Supplemental material for this article is available online.

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