

# Brain Regions Involved in Human Movement Perception: A Quantitative Voxel-Based Meta-Analysis

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**Abstract:** Face, hands, and body movements are powerful signals essential for social interactions. In the last 2 decades, a large number of brain imaging studies have explored the neural correlates of the perception of these signals. Formal synthesis is crucially needed, however, to extract the key circuits involved in human motion perception across the variety of paradigms and stimuli that have been used. Here, we used the activation likelihood estimation (ALE) meta-analysis approach with random effect analysis. We performed meta-analyses on three classes of biological motion: movement of the whole body, hands, and face. Additional analyses of studies of static faces or body stimuli and sub-analyses grouping experiments as a function of their control stimuli or task employed allowed us to identify main effects of movements and forms perception, as well as effects of task demand. In addition to specific features, all conditions showed convergence in occipito-temporal and fronto-parietal regions, but with different peak location and extent. The conjunction of the three ALE maps revealed convergence in all categories in a region of the right posterior superior temporal sulcus as well as in a bilateral region at the junction between middle temporal and lateral occipital gyri. Activation in these regions was not a function of attentional demand and was significant also when controlling for non-specific motion perception. This quantitative synthesis points towards a special role for posterior superior temporal sulcus for integrating human movement percept, and supports a specific representation for body parts in middle temporal, fusiform, precentral, and parietal areas. *Hum Brain Mapp* 33:431–454, 2012. © 2011 Wiley Periodicals, Inc.

**Key words:** fMRI; human motion; action observation; superior temporal sulcus; premotor cortex; inferior frontal gyrus; mirror neurons; social cognition

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## INTRODUCTION

Transmitting and decoding human movement signals—mainly movements of the face, body, and hands—is essen-

tial for social cognition and interaction [Brothers, 1990]. Studies in various animal species have long evidenced brain regions specialized to process social visual stimuli. Over the last 2 decades, finding the neural correlates of

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social signals perception in humans has attracted a large number of brain imaging studies. These studies, however, stemmed from various traditions and thus adopted different approaches and put emphasis on different aspects of social perception, making general syntheses difficult.

Studies focusing on core mechanisms of visual perception have often adopted a modularity approach and have emphasized the selectivity of certain brain regions, mainly in the occipito-temporal cortex, for processing specific categories of visual stimuli [e.g., Downing et al., 2001; Kanwisher et al., 1997; Peelen et al., 2005; Rotshtein et al., 2005]. In contrast, studies related to social cognition have often focused a priori on activity in the superior temporal sulcus [e.g., Allison et al., 2000; Carr et al., 2003; Pelphrey et al., 2005], where activity specific to biological motion perception has been described in human and non-human primates. Finally, another approach to human movement perception stems from embodied theories of perception, which emphasize common grounds for visual and sensorimotor information processing [Goldman and deVignemont, 2009]. Taking this perspective, many studies on action observation have emphasized the recruitment of premotor and parietal regions, and discussed this in relation to mirror neurons evidenced in homologue regions in monkeys.

Although at first glance most brain imaging studies of human movement perception seem to conform to a common general picture, implicating occipito-temporal and fronto-parietal regions, to date no formal synthesis exists and several questions remain unanswered. Apart from a few studies that have used several stimuli types [Bonda et al., 1996; Buccino et al., 2001; Grosbras and Paus, 2006; Pelphrey et al., 2005; Thompson et al., 2007], most studies used only one category of visual stimuli, that is, face or gaze stimuli, body movements or hand gestures. Therefore, it remains unclear whether some regions would be engaged by any biological motion whereas others would be specifically perceiving one body part. Also, within regions that are engaged by diverse human movement stimuli, it seems that the representation of those stimuli follows a topology similar to the somatotopy observed in motor and somatosensory cortices. This has been described in individuals and in small groups of subjects in dorsal premotor [Grosbras and Paus, 2006], ventral premotor and parietal cortex [Buccino et al., 2001], and STS [Pelphrey et al., 2005; Thompson et al., 2007] but remains to be generalized.

An important argument for synthesis of neuroimaging results is that brain imaging studies are intrinsically underpowered with typically only 10–20 subjects. Moreover, as fMRI and PET rely on indirect measures of neuronal activity, they are susceptible to several technical and biological confounds that reduce their reliability. Finally, fMRI data is particularly sensitive to the selection of task components and the contrast employed to isolate specific brain activity. Consequently, divergence in results can arise from subtle differences in design. Therefore, it is difficult to evaluate what is specific to a particular report and what would generalize across a number of contexts, tasks, stimuli, and subjects.

One way to overcome these limitations is to identify convergent regions of activation over multiple studies. Qualitative meta-analyses have been performed by plotting published maxima of activity reported in different studies on a common standard brain template and describing how they clustered: Grezes and Decety [2001] identified regions of overlap in the motor system during action execution, action simulation, and action observation. Allison [2000] described concordant report of activation within the STS during the perception of socially relevant stimuli.

Here, instead of a qualitative region-of-interest meta-analysis, we propose to perform a quantitative voxelwise random effect meta-analysis, using the activation likelihood estimation (ALE) method [Eickhoff et al., 2009; Laird et al., 2005]. This approach allows us to estimate at each location in the brain the probability that a study on human movement observation would report a focus of activity, and thus to identify regions in the brain where the convergence across studies is maximal.

We restricted the meta-analysis to experiments on observation of movements, without subsequent or simultaneous imitation, focusing on the differences between the different effectors and the contextual modulation of brain activation. Two recent meta-analyses have reviewed imitation and action observation studies across a variety of stimuli, with the aim of comparing the sets of regions involved in both domains [Caspers et al., 2010; Molenberghs et al., 2009]. Given the different focus, the inclusion criteria of these analyses were less specific regarding the human movement perception aspect, leading them to consider also studies using auditory or linguistic stimuli or using emotional material. Moreover, studies using different categories of stimuli were not always separated from each other and specific properties of the control conditions were not always considered. Contrary to those two previous studies we here focus on the regions that are involved in human form and motion perception. Importantly, we did not include emotional stimuli nor higher level processes, such as theory of mind, to concentrate on the perception of human movements and experimental factors that may influence brain activity.

Task and attentional demands are key factors that have been shown to modulate the regions recruited during action observation [e.g., Cohen-Khadosh et al., 2009]. To investigate this, at the level of the meta-analysis, we performed sub-analyses asking whether some regions are more likely to be reported in studies of action observation that use a purposeful task as compared to those that use passive observation or vice versa. The intention of the agent is another important modulator of mechanisms engaged during human movements perception. In particular, goal-directed, symbolic, and meaningless movements have been reported to evoke different patterns of brain activation [Decety et al., 1997; Gallese et al., 1996]. We aimed to address this question here at the meta-analytic level, which in practice was possible only for hand movements given the paucity of studies investigating transitive mouth or body movements.

We were primarily interested in dynamic stimuli, as these are involved in everyday social interaction. Interpreting such signals requires decoding both form and movement information [Jastorff and Orban, 2009]. However, reviewing the literature revealed an important bias in the questions and analysis methods used: whereas studies interested in face movements frequently use static faces as controls, movements of bodies and hands are most often contrasted to either non-biological motion or a blank screen. Therefore, the results of studies of face movements may emphasize biological movement while minimizing the effect of form, whereas the studies of body or hand movements potentially reveal activity that is related to both human form and movement perception. To remedy this bias and disentangle brain regions sensitive to either human form or motion, we conducted two separate meta-analyses; one of experiments contrasting static faces to non-biological stimuli and one of experiments contrasting static body or body parts to non-biological stimuli.

In summary, our general goal was to identify brain regions that are reliably engaged during the perception of human movements. This allowed us to delineate commonalities and differences across three categories of movements: those of the whole-body, the hands, and the face. Such quantitative synthesis also provides landmark coordinates for regions of maximum convergence across studies, which can be used to discuss future brain imaging results or consequences of brain lesion, as well as for planning non-invasive brain stimulation studies to further investigate the role of these regions in social perception.

## METHODS

### Selection of Studies for the Meta-Analysis (Tables I and II)

The primary research question aimed at identifying the brain areas consistently implicated in viewing hands, face, and whole body motion. Databases, as available in Web of Knowledge (Thompson Reuters), were searched using the keywords “fMRI” or “PET,” accompanied by relevant terms, namely: “biological motion,” “action observation,” “human movement,” “face movement,” “gaze perception,” as of 19th May 2010. We selected only studies that used dynamic stimuli; these could include videos, virtual reality animations, or point-light displays. Articles were required to report 3D stereotaxic coordinates for whole-brain analyses based on either the MNI or Talairach template. Finally, we excluded experiments on drug effects and those that focused on “special populations,” such as children or clinical conditions.

We excluded experiments including overt movement of the participants or explicit instruction of motor imagery. In one study [Lui et al., 2008], the explicit motor imagery condition, without visual input, served as a control condition. We kept this study as it extracts processes involved in action observation but not in motor imagery.

Body movements included stimuli containing point-light motion (nine studies) and real videos (ten studies); for the full-light stimuli, only studies where the face was not visible or blurred were included.

Studies of facial movements comprised three kinds of stimuli: whole face movements (without emotional expression); mouth movements (simple mouth movements like opening or closing, but also some speech-related movements); and gaze movement.

The condition of hand-movement observation consisted in a higher number of experiments, which allowed us to divide it into two subcategories: object-related (transitive) and non object-related (intransitive) movements. The latter category included hand movements that mimicked object manipulation (four studies) as well as communicative hand movements (two studies). All stimuli included the hand and often also showed a variable degree of the arm and rarely parts of the trunk.

As we could identify only three suitable studies of observation of legs or foot movement, we did not analyze this category.

The control condition had to be a stimulus without biological motion or a blank screen. As can be seen in Tables I and III, the control conditions can be classified into four different categories: non-biological motion, static human stimulus, static non-human stimulus, or blank screen. We first performed general meta-analyses pooling studies across the different control conditions. These reveal regions that are consistently reported as activated when viewing movements of the whole body, face, or hand, across a variety of contrasts. The assumption is that those regions contain neurons engaged in common computational processes shared by the experimental conditions but not their respective controls, that is, human movement perception. To be more specific with respect to the processes revealed by this meta-analysis, and to compare the effects of different control conditions, we performed sub-analyses within each category grouping together studies according to the control conditions they used.

In about half of the experiments that were included in this meta-analysis, the instruction was to passively observe the stimuli (see Tables I and III). In the other half of the experiments, attention load was increased by asking participants to complete a task involving memory or judgment. We contrasted those two kinds of studies (passive and task) in separate sub-analyses.

Moreover, to gain further insight into the brain regions engaged while watching human stimuli, independently of their movement, we computed two additional meta-analyses: one of experiments contrasting static faces to objects or low-level visual stimuli, and the other of experiments contrasting static body or body parts to objects or low-level visual stimuli. In contrast to the different sub-group analyses and contrasts performed on the main set of experiments (detailed in Tables I–III), this meta-analysis was based on a separate literature search on studies reporting brain activity related to the observation of static

**TABLE I. Studies entered into the Meta-analysis**

Ref.	Meth.	N	Stimuli	Task	Control	Example of stimulus
<b>Body movements</b>						
Beauchamp et al., 2003	3T	9	Whole-body motions filmed from different viewpoint	Forced-choice discrimination task	Video clips of tool motion	
Bonda et al., 1996	PET	11	Point-light displays of dance-like movements	Watch and recognize afterwards	Random motion dot patterns	
Calvo-Merino, 2005	3T	20	Dance movements	Rate how tiring movement is	Blank screen	
Cross et al., 2006		17	Dance movements	Rate own ability to perform movement	Fixation in blank screen	
Grezes et al., 2001	1.5T	10	Point-light walker	Observe	Random dot cube rotating	
Grezes, 2007	1.5T	16	Opening a door	Detect oddball stimulus (upside-down video clip)	Static frames from videos	
Grossman and Blake, 2002	3T	10	Point-light walker	Observe	Scrambled point-light animations	
Howard et al., 1996	1.5T	6	Point-light video of running man	Observe	Random motion of dots	
Iseki et al., 2008	3T	16	Normal gait movements	Watch very carefully	Movie of scrambled frames	
Jung et al., 2009	1.5T	15	Point-light kicking, throwing, running, climbing, jumping	1-back task	Scrambled point-light animations	
Michels et al., 2005	1.5T	4	Point-light walker	Detect human figure	Detect luminance change in stationary dots	
Peelen et al., 2006	1.5T	18	Animations of simple, whole-body actions	Observe	Scrambled images of the same animations	
Peuskens et al., 2005	1.5T	6	Point-light animations of different human actions	Observe, with central fixation	Scrambled animations	
Pichon et al., 2008	1.5T	16	Actor opening and closing a door	Detect oddball	Static frames from videos	
Santi et al., 2003	4T	10	Point-light animations of jumping and walking	Observe, with central fixation	Scrambled version of point-light walker	
Saygin et al., 2004	4T	12	Point-light biological motion animations of 10 actions	Detect color of dots	Scrambled versions of the same animations	
Servos et al., 2002	4T	16	Point-light animations of jumping and walking	Detect degrade motion	Scrambled version of point-light walker	

TABLE I. (Continued)

Ref.	Meth.	N	Stimuli	Task	Control	Example of stimulus
Thompson et al., 2005	3T	10	Animated mannequins walking	Detect gait changes; central fixation	Body parts of the mannequin displayed apart	
Zentgraf et al., 2005	1.5T	10	Gymnastic movements	Judge quality or observe to imagine afterwards	Blank screen	
Vaina et al., 2001	1.5T	5	Point-light walker	Observe	Discrimination on briefly flashed letters T and L	
<b>Hand movements (non-object related)</b>						
Bonda et al., 1996	PET	11	Point-light display of hand simulating grasping	Observe and report afterwards	Random motion of point lights	
Buccino et al., 2001	1.5T	12	Hand mimicking action	Observe	Static hand	
Costantini et al., 2005	1.5	13	Index or little finger movement	Observe	Moving scissors	
Cunnington et al., 2006	3T	14	Finger movements from the ASL (that could be known or unknown)	Observe to imitate subsequently	Scrambled image	
Gallagher and Frith, 2004	2T	12	Expressive and instrumental hand gestures	Observe	Still frame of neutral gesture	
Grezes et al., 1998	PET	10 (males)	Meaningless hand movement	Observe	Static hand	
Grezes et al., 1999	PET	9 (males)	Meaningless hand movements (derived from ASL)	Conjunction passive viewing and observe to imitate afterwards	Static hand	
Holle et al., 2010	3T	16	Narrative gestures	Observe	Fixation	
Jonas et al., 2007	3T	17	Finger movements	Watch and lift finger when oddball stimulus appear	Static hand	
Lui et al., 2008	1.5T	16	Mimed action, symbolic or meaningless movements 2 s clips	Carefully watch and extract meaning if present	Blue screen and motor imagery of the action that has just been shown	
Montgomery et al., 2007	3T	14 (males)	Mimed action 2 s clips	Observe	Blank screen	
Thompson et al., 2007	3T	11	Synthesized Index finger movements. Blocks of 40 s	Detect a target sequence of movement	Radial grating expanding and contracting	

TABLE I. (Continued)

Ref.	Meth.	N	Stimuli	Task	Control	Example of stimulus
Villarreal et al., 2008	1.5T	17	Meaningless gestures of right arm and hand	Observe to recognize afterwards	Fixation in blank screen	
Wheaton et al., 2004	3T	12	Opening and closing	Observe with central fixation	Static hand	
<b>Hand movement (object-related)</b>						
Aziz_Zadeh et al., 2006	3T	12	Reaching and grasping	Observe	Blank screen	
Baumgartner et al., 2009	3T	19	Manipulating object 2s videos	Pay attention to the adequacy of the action	Object moved by mechanical power (e.g. tumble dryer)	
Biagi et al., 2010	1.5T	12	Manipulating object with right or left hand 8 s videos	Observe with central fixation	Static hands and object	
Buccino et al., 2000	3T	12	Reaching and grasping a ball or a cup	Observe	Static hand	
Buccino et al., 2004	1.5T	12	Hand performing guitar chord	Observe	Blank screen	
Cheng et al., 2007	3T	10	Hand reaching and grasping. 2.5 s clips	Observe and report afterwards	Scrambled picture of object	
Chong et al., 2008	1.5T	16	Hand reaching and grasping	Observe and discriminate which grip is used	Diamond shapes and discriminate color	
Filimon et al., 2007	3T	16	Reaching and grasping object with abstract shape	Observe, with central fixation	Stationary object	
Gazzola et al., 2007	1.5T	16	Reaching, grasping, and manipulating object on a table	Pay attention to hand-object relationship	Static object and arm and hand behind it	
Grafton et al., 1996	PET	7	Experimenter's hand grasping objects	Observe	Object in hand, without movement	
Grosbras and Paus, 2006	1.5T	20	Reaching, grasping, and manipulating objects	Observe to recognize afterwards	Expanding and contracting circles	
Lotze et al., 2006	fMRI 1.5T	20	Meaningful movements (50% with object present and 50% pantomime)	Observe	Blank screen	
Meister and Iacoboni, 2007	3T	14	Hand manipulating object	Count number of finger touching object	Blank screen	
Molnar-Szakacs et al., 2006	3T	12	Sequence of four movements manipulating an object	Watch and pay attention to object manipulation	Blank screen	
Perani et al., 2001	PET	8	Hand grasping geometrical objects	Observe	Stationary objects	
Pierno et al., 2006	3T	14	Actor reaching and grasping an object	Observe	Stationary object	

◆ Meta-Analysis of Movement Observation Circuits ◆

TABLE I. (Continued)

Ref.	Meth.	N	Stimuli	Task	Control	Example of stimulus
Shmuelof et al., 2005	1.5T	11	Hand reaching, grasping, and releasing an object	Observe with central fixation	Movie of scrambled images	
Schuboz and Von Cramon, 2004	3T	18	Both hands performing actions that involved two objects	Observe report afterwards	Movie with changing objects	
Schubotz and Von Cramon, 2009	3T	18	Hand actions involving two objects appropriately or not	Observe. In 25% of trials, prompt for response	Blank screen	
Tai et al., 2004	PET	7	Experimenter's hand grasping an object	Observe	Static hand	
Turella et al., 2009	3T	17	Reaching and grasping	Observe	Blank screen with fixation	
<b>Face movements</b>						
Whole face movements						
Fox et al., 2009	3T	16	Moving faces	One-back task	Moving objects	
Grosbras and Paus, 2006	3T	20	Non-emotional face movements	Observe and report afterwards	Concentric circles expanding and contracting	
Kilts et al., 2003	PET	13	Dynamic faces	Judge position of face relative to centre	Static faces	
Lee et al., 2009	3T	17	Head turning	Observe and detect a rare red dot	Movie of scrambled frames	
Eye movements						
Hooker et al., 2003	fMRI 1.5T	10	Averted gaze shifts and back to centre	Monitor eye-gaze target	Moving arrow on a static face	
Pelphrey et al., 2005	fMRI 4T	15	Animated characters Averted gaze shifts and back to centre	Observe	Still frame of character	
Puce et al., 1998	fMRI 1.5T	11	Averted gaze shifts	Attend and focus on a point midway between the eyes	Static face with moving radial background	
Pierno et al., 2006	fMRI 3T	14	Gaze away and towards an object	Observe	Actor still with eyes away from object	
Wicker et al., 1998	PET	10	Averted gaze shifts and back to centre	Observe	Static face looking down (only eye id visible)	
Mouth movements						
Aziz_Zadeh et al., 2006	3T	12	Side view of mouth biting a fruit	Observe	Blank screen	

**TABLE I. (Continued)**

Ref.	Meth.	N	Stimuli	Task	Control	Example of stimulus
Buccino et al., 2001	1.5T	12	Mime mouth actions (biting an apple and chewing)	Observe	Static face	
Calvert and Campbell, 2003	3T	8	Lower half of a face uttering consonant and vowel syllables	Fixate mouth area and detect phoneme target	Closed mouth images	
Calvert et al., 1997		7	Lip movements of spoken or mouthed numbers	Lip-reading	Static face	
Campbell et al., 2001	1.5T	7	Numbers spoken by a female face	Rehearse silently the number	Static face. Count silently	
Fridriksson et al., 2008	3T	20	Speech and non-speech mouth movements	Same-different judgement	Blank screen	
Hall et al., 2005	3T	33	Face grunting	Press a key after each video	Static face with closed mouth	
Paulesu et al., 2003	PET	8	Backward video of a face speaking	Observe and refrain from articulation	Static face	
Pelphrey et al., 2005	4T	15	Animated character opening and closing his mouth	Observe	Still of character	
Santi, et al., 2003	4T	10	Point-light animation of face speaking	Observe with central fixation	Scrambled dots patterns	
Thompson et al., 2007	3T	11	Animated face opening mouth	Central fixation and detect target sequence of movements	Radial grating motion	
Wheaton et al., 2004	3T	12	Opening and closing mouth	Observe	Static face	

Meth = method: fMRI field strength or PET; N = number of subjects.

faces, body, or body parts. When retrieving the relevant studies, the same inclusion and exclusion criteria (apart obviously from those applying to the stimuli) as reported above for the main analysis were applied. Details on the experiments that were included in these additional analyses are listed in Table VI. Meta-analysis approaches did not differ between the main analysis, sub-group analyses, and the additional analyses on experiments using static stimuli. The description of the meta-analysis algorithm described below thus pertains to all analyses indicated above.

### Analysis

We used the ALE method to conduct a random effect analysis of the convergence between studies [www.brainmap.org; Eickhoff et al., 2009; Laird et al., 2005]. For each condition of interest we identified a number of experiments matching our criteria (Table II). Coordinates reported in Talairach—rather than MNI-template—were converted using the Tal2ICBM function [Lancaster et al., 2007]. Foci outside of a mask of gray matter [ $>10\%$  probability

for gray matter, based on the ICBM tissue probability maps; Evans et al., 1994], were excluded from analysis. Then for each experiment, each reported maximum was modeled as a Gaussian distribution with a full-width half-maximum (FWHM) estimated based on empirical between-template and between-subjects variance [Eickhoff et al., 2009] and scaled by the number of subjects who had participated in this experiment. Merging the derived probability values yielded one 3D “modeled activation” map

**TABLE II. Number of experiments and foci included in each condition**

Condition	No. of experiments	Total no. of subjects	Mean no. of subjects	No. of foci
Body	20	237	11.8	234
Hand	14	184	13.1	112
Hand-Object	21	291	13.8	283
Faces	21	281	13.4	267
Mouth	12	155	12.9	154
Eyes	5	60	12	43

**TABLE III. Different kinds of contrasts and number of experiments using them within each movement observation category**

Contrast	Moving social > static social	Moving social > moving non-social	Moving social > static non-social	Moving social > blank	Passive observation	Task	Static social > static non social
Isolated process	Human movement	Human form and movement	Human form and movement + non-specific movement	Human form and movement + non-specific form and movement	Free attention	Attention to the effector	Human form
Body	3	10	4	3	9	11	–
Hand	6	3	1	4	8	6	–
Hand-object	5	4	5	7	10	11	6
Faces	14	4	1	2	10	10	16

per experiment. Those maps are then combined by taking the voxel-wise union of them to produce an ALE map, which reflects the probability that any focus is located within a given voxel. To establish which regions were significantly activated across experiments, these ALE scores were compared to a null-distribution that reflects a random spatial association between experiments, but regards the within-experiment distribution of foci as fixed [Eickhoff et al., 2009]. This random-effects inference assesses above-chance convergence between experiments, not clustering of foci within a particular experiment. The “true” ALE scores were then tested against the ALE scores obtained under this null-distribution yielding a *P* value based on the proportion of equal or higher random values. The resulting non-parametric *P* values were transformed into *Z* scores and thresholded at  $P < 0.001$  and cluster extent of 120 mm<sup>3</sup>. This combination of height- and extent-threshold provides solid protection against false positives, and no formal correction for multiple comparisons was performed due to limited power for the analyses that included a limited number of experiments. In particular, controlling the family-wise error (FWE) would have been unduly conservative in some of the smaller analyses, whereas the validity of false discovery rate (FDR) correction in the context of neuroimaging meta-analyses has been fundamentally questioned recently [Chumbley et al., 2009, 2010]. To identify regions implicated by two different meta-analyses, we performed a conjunction analysis by computing the minimum statistic on the thresholded results maps (i.e., intersection between significant ALE maps).

Differences between conditions were tested by first performing an ALE analysis separately for each condition and computing the voxel-wise difference between the ensuing ALE maps. All experiments contributing to either analysis were then pooled and randomly divided into two groups of the same size as the two original sets of experiments (i.e., Condition 1 and Condition 2). ALE-scores for these two randomly assembled groups were calculated and the difference between these ALE-scores was recorded for each voxel in the brain. Repeating this process 10,000 times then yielded a null-distribution of differences in ALE-scores

between the two conditions. The “true” difference in ALE scores was then tested against this null-distribution yielding a *P* value for the difference at each voxel, based on the proportion of equal or higher random differences. The resulting non-parametric *P* values were transformed into *Z* scores, thresholded at  $P < 0.05$  and inclusively masked by the respective main effects, that is, the significant effects of the ALE analysis for the particular condition.

Results maps were overlaid on a standardized high-resolution structural scan for macroanatomical localisation. Moreover, clusters of significant convergence were superimposed on probabilistic cytoarchitectonic maps to characterize their overlap with histologically defined areas in the region of V5 [Malikovic et al., 2007], the somatosensory cortex [Eickhoff et al., 2006a,b; Grefkes et al., 2001], the intraparietal sulcus [Choi et al., 2006] as well as the inferior parietal [Caspers et al., 2008] and frontal [BA 44 and BA 45; Amunts et al., 1999, 2004] cortices.

## RESULTS

### Body, Hand, and Face Movement Perception

Table II shows the number of experiments and foci included for each condition. Table IV shows the coordinates for maxima in the clusters of significant convergence.

For the body movements perception condition (Fig. 1A), the highest ALE scores and largest clusters were observed, in both hemispheres, in the lateral occipito-temporal cortex, with the maxima around the location described as the extrastriate body area (EBA) [Downing et al., 2001]. These clusters overlapped with the cytoarchitecturally defined area MT/V5 and extended into the middle temporal gyrus (MTG) and posterior superior temporal sulcus (STS). Large clusters were also observed in the fusiform cortex, with dominance in the right hemisphere.

For the intransitive hand movement perception (Fig. 1B), the highest ALE score was in the lateral temporal and occipital cortex, bilaterally, encompassing area MT/V5, and a large amount of the MTG. These clusters extended dorsally into the posterior STS and ventrally into the

TABLE IV. Clusters of significant ALE for the four different conditions

Region	Side	X	Y	Z	ALE score	Z score
Body movements						
Temporal lobe						
Lat. Occ./Inf. Temp. G	R	48	-70	-6	21.91	5.50
	L	-48	-72	-4	14.91	4.19
MTG/Angular G.	R	58	-52	12	19.16	4.99
SMG	R	56	-38	20	13.50	3.93
Middle Occipital G	R	30	-92	6	3.70	3.70
	L	-30	-92	8	3.98	3.65
Occipital Pole	R	16	-98	0	11.55	3.51
Inf. Temporal G	L	-44	-72	0	14.52	4.40
	L	-46	-68	8	8.71	4.56
Angular G.	L	-44	-56	16	12.25	3.59
Fusiform G.	R	40	-40	-20	8.77	3.22
	R	44	-52	-22	8.02	4.24
	L	-36	-44	-16	10.72	3.87
Occipital Fusiform G.	R	36	-72	-20	17.11	4.33
Parietal lobe						
Parietal Operculum/SMG	R	58	-30	34	14.44	3.37
	L	-58	-38	28	18.19	5.37
SPL/IPS		60	-28	30	12.05	3.63
	R	32	-40	48	7.50	4.03
	L	-36	-38	38	11.58	3.18
Hand movements						
Temporal lobe						
Inf. Temp. G./Lat. Occ.	R	48	-66	-2	19.99	5.39
MTG	R	52	-60	6	16.97	4.81
	L	-48	-68	6	20.18	5.43
STG	R	56	-42	10	11.49	3.73
	L	-56	-52	10	19.30	5.26
STS	R	48	-40	2	10.76	3.58
Fusiform G.	L	-42	-62	-12	13.21	4.10
Occ. Pole/ Lingual G.	L	-14	-98	-2	12.34	3.90
Parietal lobe						
Ant. IPS /Postcentral	L	-40	-38	40	21.35	5.62
SMG	R	60	-22	42	10.00	3.43
SPL	R	34	-48	58	15.00	4.49
Frontal lobe						
S. Prec.	R	50	-2	46	11.11	3.65
I. Prec.	L	-52	8	20	12.81	4.01
Object-directed hand movements						
Temporal lobe						
MTG/Lat. Occ.	R	48	-64	4	30.08	6.07
		-52	-62	12	16.90	4.06
Inf. Temp. G./Lat. Occ. (V5)	R	48	-66	0	28.13	5.79
	L	-44	-70	2	34.43	6.66
Fusiform G.	R	42	-48	-20	22.28	5.01
	L	-42	-50	-20	17.38	4.14
Sup Lat. Occ.	L	-20	-86	34	15.35	3.80
Parietal lobe						
Anterior IPS/Postcentral	L	-58	-28	38	23.60	5.13
IPS (hIP1)	R	36	-44	54	24.85	5.34
	L	-36	-42	54	29.51	5.99
SPL	R	22	-64	64	16.64	4.01
	L	-30	-52	64	21.29	4.78
	L	-28	-52	46	21.38	4.80
SMG	R	50	-40	22	14.46	3.64

TABLE IV. (Continued)

Region	Side	X	Y	Z	ALE score	Z score
Frontal lobe						
S. Prec (BA 6)	L	-24	-6	58	27.28	5.68
	R	34	-4	56	23.08	5.06
	R	48	2	46	18.71	4.36
I. Prec.	R	48	14	24	19.70	4.52
	L	-54	8	28	22.01	4.89
IFG (p triang, BA45)	R	54	28	18	22.04	4.89
Post. Cingulate G.	R	14	-22	44	14.95	3.73
	L	-14	-24	40	14.93	3.73
Subcortical						
Thalamus	L	-16	-24	8	15.68	3.86
Cerebellum	R	12	-76	-48	12.87	3.33
	L	-12	-78	-46	16.24	3.94
Face movements						
Temporal lobe						
MTG/pSTS	R	50	-58	8	30.11	6.40
	L	-50	-52	6	28.72	6.19
	L	-48	-62	14	15.52	5.13
MTG/Lat Occ	R	44	-72	0	19.12	4.69
	L	-40	-74	4	18.27	4.55
Lat. Occ.	R	46	-72	-12	14.47	3.87
	L	-46	-70	-4	20.41	4.91
Middle Occipital Gyrus	R	26	-88	0	13.87	3.76
	R	58	-32	8	18.02	4.50
STG	R	56	-46	4	26.24	5.82
	R	54	-4	-14	13.42	3.66
Ant STS	R	54	-4	-14	13.42	3.66
Fusiform G.	R	46	-56	-22	13.42	3.65
Frontal lobe						
S. Prec (BA6)	R	48	2	46	17.46	4.41
	L	-42	-4	54	14.14	3.79
I. Prec/ IFG (pars op.; BA44)	R	52	12	18	14.83	3.92
	L	-42	12	26	19.50	4.76
IFG (BA45)	R	56	24	20	14.40	3.85
Pre-SMA (BA6)	R	2	10	60	16.85	4.32
Ant. Cingulate G.	L	-2	18	42	12.42	3.45

Coordinates in MNI space, ALE scores ( $\times 10^3$ ) and Z Scores are given for the voxel with highest score within each cluster.

IFG, Inferior Frontal Gyrus; iPrec, Inferior Precentral Gyrus; IPS, Intraparietal Sulcus; Lat Occ, Lateral Occipital Gyrus; MTG, Middle Temporal Gyrus; PPC, Posterior Parietal Cortex; pSTS, Posterior Superior Temporal Sulcus; SPL, Superior Parietal Lobule; SMG, Supramarginal Gyrus; sPrec, Superior Precentral Gyrus; SFG, Superior Frontal Gyrus; MFG, Middle Frontal Gyrus.

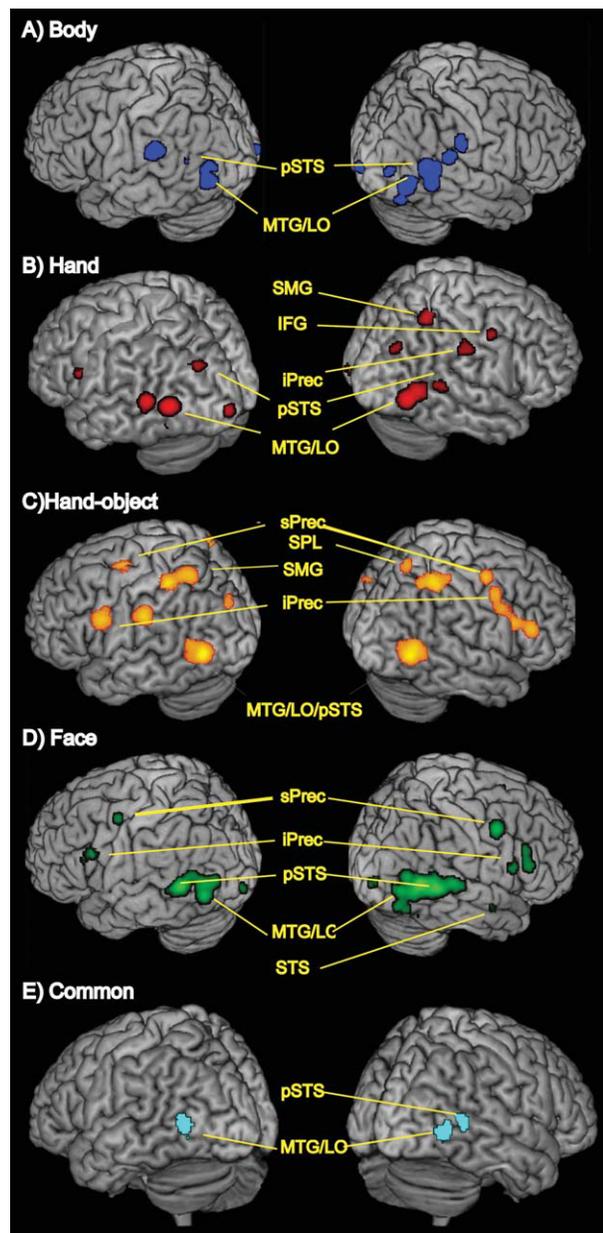
lateral occipital cortex, again with a right hemisphere dominance. Smaller clusters were observed in posterior and anterior parietal cortices (supramarginal gyrus and intraparietal sulcus, at the border between BA2 and hIP2), in the right superior and left inferior precentral cortex and the inferior frontal gyrus (IFG, Brodman Area 44). Studies on observation of object-directed hand movements yielded significant convergence in overlapping but larger clusters than those on intransitive hand movements (Fig. 1C). Additional clusters could be seen in the IFG (Brodman Areas 44 and 45), posterior cingulate, precuneus, and cerebellum.

For the face movement perception (Fig. 1D), the highest ALE scores were observed in the MTG and the posterior STS bilaterally. The next most significant clusters were located in

the inferior precentral cortex (BA 6) and the inferior frontal gyrus *pars opercularis* (BA44) bilaterally, as well as in the right IFG *pars triangularis* (BA45) and on the medial premotor cortex (pre-Supplementary Motor Area, BA6).

### Static Body and Face Perception

To isolate regions specifically involved in face-shape perception, we performed an independent meta-analysis on 16 experiments (179 foci) reporting contrasts between viewing photographs of faces and viewing objects or scrambled images. This set of studies was matched with the set of studies included in the main analysis with respect to the



**Figure 1.**

Significant ALE scores rendered on a high-resolution template in MNI space, for each individual movement observation category. Brightest colors correspond to higher ALE scores. (A) Body movement, (B) Hand movements, (C) Object-directed Hand movements, (D) Face movements, and (E) Shows significant ALE for the conjunction of all the above observation conditions, that is, the regions where ALE was significant in all four results maps. IFG, Inferior Frontal Gyrus; iPrec, Inferior Precentral Gyrus; IPS, Intraparietal Sulcus; LO, Lateral Occipital Gyrus; MTG, Middle Temporal Gyrus; PPC, Posterior Parietal Cortex; pSTS, Posterior Superior Temporal Sulcus; SPL, Superior Parietal Lobule; SMG, Supramarginal Gyrus; sPrec, Superior Precentral Gyrus. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

complexity of stimuli and task demands (see Table VI). Convergence was significant in most regions identified in the meta-analysis of movement perception, and also in bilateral amygdala, posterior cingulate cortex, left fusiform, and right superior frontal gyrus (Table VII and Fig. 3).

To delineate regions more sensitive to moving than static faces, we computed a contrast between the 14 studies that have contrasted moving to static faces and those reporting static faces versus non-face control stimuli. This direct comparison revealed significantly stronger convergence for face movement than face shape in the middle temporal/lateral occipital gyrus, right posterior STS, right dorsal premotor cortex, and inferior frontal gyrus (IFG; BA 44).

We could identify six experiments (53 foci) that contrasted static body or body parts (including hands) to non-social stimuli and were suitable for a meta-analysis. In this analysis, the highest ALE scores were at the same locations as the moving body condition, but activity in the cluster located in lateral occipital gyrus and inferior temporal gyri extended more laterally and dorsally in both hemispheres (see also Table VII and Fig. 3).

#### Significant Convergence Common to All Conditions

The conjunction of the four movement conditions reported above (body, transitive and intransitive hand, and face movements) revealed significant common convergence at the junction between the middle temporal gyrus (MTG), inferior temporal sulcus, and lateral occipital gyrus (Fig. 1D;  $x = 48, y = -66, z = 0$  mm and  $x = -48, y = -70, z = 4$ , 46% overlap with right and 30% with left cytoarchitecturally defined V5). In addition we observed another site of common convergence more dorsal and more anterior in the right posterior temporal sulcus/gyrus (pSTS:  $x = 54, y = -54, z = 10$  mm).

Given the heterogeneity of included contrasts, this common convergence may be driven by movement perception per se, rather than human movement specifically. To address this issue, we conducted a separate meta-analysis across all experiments that used moving stimuli as control and thus minimized the effect of non-specific motion. This analysis included 21 experiments (Table III) and was performed with the same statistical and thresholding procedures as the main analysis. Results are summarized in Table VIII. To restrict inference to those regions that were responsive to human movement, we here used the results from the conjunction analysis [i.e., voxels with significant convergence ( $P < 0.001$ ) in all conditions] as a mask. That is, we tested for the voxels activated in the four conditions of the main analysis whether there was significant activation (at  $P < 0.001$ ) for the contrast between human motion and moving control stimuli. The three regions identified in the conjunction analysis also showed significant convergence in this analysis, indicating that the common activation is indeed due to human movement perception.

Moreover, it may be argued that this activation may be more related to the presence of a human shape rather than human movement. To investigate the extent to which the concordant convergence is driven by human form perception rather than movement, we then investigated whether static stimuli produced activation in the same loci. Again, we used results from the conjunction analysis as a mask for the results of the separate meta-analyses conducted on studies of static stimuli (thresholded at  $P < 0.001$ ). The meta-analysis on static face perception relative to non-human control stimuli revealed significant effects within the right MTG/occipital regions revealed in the conjunction analysis as well as in a handful of right pSTS voxels revealed in the conjunction analysis. As can be seen in Figure 3, the pSTS cluster identified in the static faces meta-analysis extends more anteriorly and dorsally relative to the region identified in the conjunction analysis. The meta-analysis on static body or body-parts perception revealed activation within the two MTG /occipital regions commonly engaged during all the movements perception conditions. It should be noted, however, that the regions showing significant convergence in the meta-analyses of static stimuli and those revealed by the conjunction analysis did not overlap completely, as can be seen in Figure 3.

To explore this issue even further, we then performed additional meta-analyses over only the subsets of studies that contrasted human movement perception to (static) human shape for the hand (11 experiments) and face (14 experiments) conditions (see Table VIII for complete account of results). The restricted analysis of face condition yielded significant convergence in all three regions identified in the conjunction. The restricted analysis of the hand condition produced significant convergence ( $P < 0.001$ , extent threshold 15 voxels) in the two posterior regions but not in the pSTS.

Finally, directly comparing studies that have contrasted moving to static faces and those reporting static faces versus non-face control stimuli revealed significantly stronger convergence ( $P < 0.05$ ) for face movement than face shape in both right hemispheres regions (MTG/occipital and pSTS) revealed in the conjunction analysis.

### Activation Specific to Only One Condition

To compare the different categories (body, hand, and face) directly, we computed new analyses restricted to a subset of studies for each category such that the contrasts of interest could be closely matched across categories. This led us look at studies that used non-biological stimuli as control conditions, including 17 experiments for the body condition, eight for hand, and six for faces. The results of these analyses were very similar to the original ones, except that we also observed significant amygdala and left fusiform convergence for face perception. We then computed for each category the conjunction of the two comparisons against the other categories. For example, the conjunction “Face > Hand” and “Face > Body” was used to identify regions specific for face movement. We

observed specificity for faces in the right middle STS ( $x = 54, y = -4, z = -12$ ), the left Inferior Frontal Gyrus pars opercularis ( $x = -50, y = 20, z = 22$ , at the border between BA 44 and 45), and the pre-SMA ( $x = 2, y = 10, z = 58$ ). We observed specific activation convergence for Hand in the left and right parietal cortex ( $x = -40, y = -30, z = 40$ ; area hIP2 and  $x = 60, y = -24, z = 40$ , BA2). We didn't observe any regions that showed significantly higher convergence for body movement perception than both face and hand movement perception.

### Topographical Organization in STS, Precentral, Parietal, and Fusiform Cortices

In the same analysis (on subsets of studies with matched control), we observed that within the MTG and posterior STS regions, studies of body perception movement yielded maximum convergence more posteriorly, laterally, and dorsally (extending into the angular gyrus) than studies of hand or face movement perception. Perception of face movements yielded maximal convergent activation in more lateral and dorsal parts of the STS than perception of hand movements (c.f., Fig. 2).

In the fusiform cortex, face movements were represented posterior to body movements with some overlap (c.f., Fig. 2,  $Z = -20$ ). The convergence for intransitive hand movements was not significant in this region but object-directed hand movements produced significant convergence overlapping with the area of convergence for whole-body movement perception.

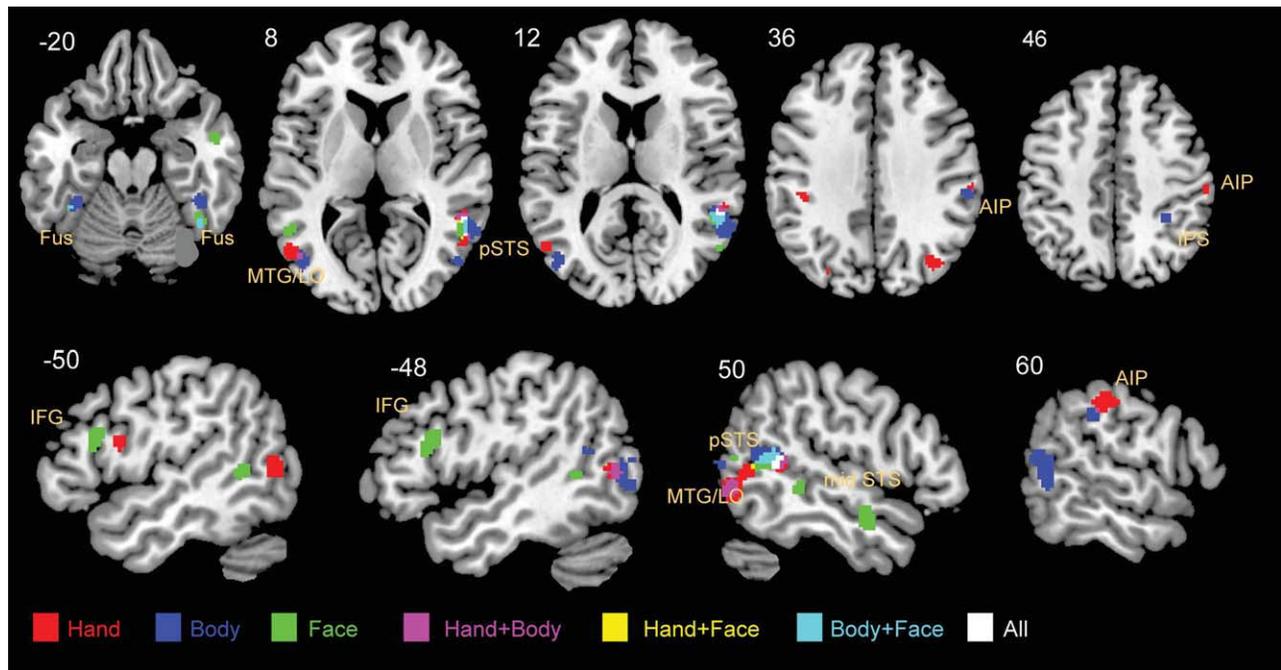
In the parietal cortex, only hand and body conditions showed concordant activation. Along the intraparietal sulcus, the hand conditions showed more extended region of convergence than the body condition, the latter producing a maximum in a distinctly more ventral and medial part of the sulcus (Fig. 2, slice  $x = 56$ ) with very little overlap between the two thresholded maps. In the inferior parietal cortex, hand movement observation was represented anterior and lateral to body movement observation.

In the frontal lobe, face and hand movement observation yielded overlapping yet topographically distinct results in the superior and inferior precentral cortices. In the left ventral premotor cortex and IFG, face movement observation was represented more rostrally extending into BA 45, whereas hand observation was confined in more caudal region restricted to BA 44

Overlapping convergence in right superior precentral gyrus was seen between hand-object and face movements perception. Closer inspection revealed that it was mainly due to experiments on gaze perception.

### Comparison of Hand and Hand-Object Conditions

In our sample of studies (Table I), the experiments included in the hand and hand-object conditions were



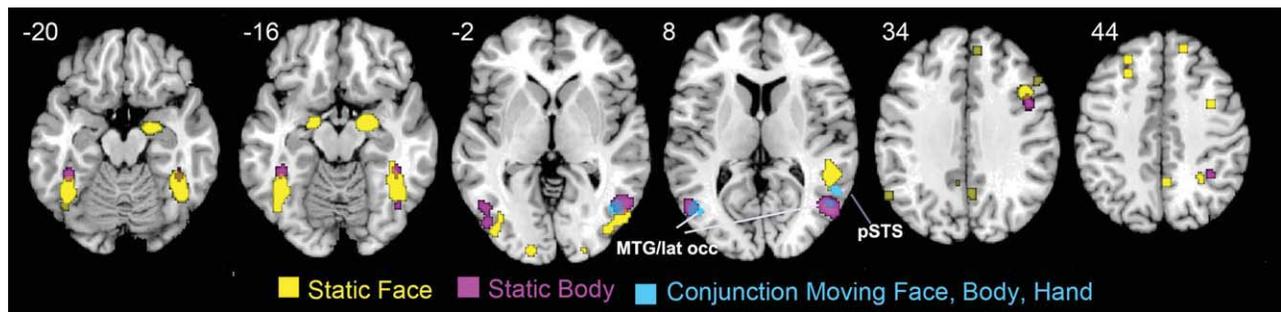
**Figure 2.**

Topographical representation of the perception of different effectors. Color codes correspond to results of meta-analyses performed on a subset of studies such that their control conditions are matched across categories (c.f., methods section), or their conjunction. Results maps (main contrasts and conjunction) are binarized and only significant voxels are represented by a

single color, as indicated in the legend. They are presented on a high-resolution structural scan. Top: axial slices with Z coordinates in MNI space; bottom sagittal slices with X coordinates. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

matched regarding the task (i.e., the same proportion of experiments with versus without a task for both conditions) as well as for the control conditions (Table III). This verified, we performed a direct contrast between the two conditions, restricted to regions that showed significant

ALE score in at least one of the two conditions. Higher convergence for object-directed hand movements was observed in the dorsal and ventral precentral cortex (BA 6), bilaterally, in the right IFG pars opercularis (overlapping with BA 44), IFG pars triangularis (BA45), anterior



**Figure 3.**

Results of the meta-analyses of studies comparing static faces to control (in yellow) and studies comparing static body or body parts to control (in pink), both thresholded at  $P < 0.001$  with a cluster extent of  $120 \text{ mm}^3$ . Also, overlaid on the same template are the results of the conjunction analysis, in blue, that is voxels that showed significant convergence ( $P < 0.001$  and cluster

extent  $>120 \text{ mm}^3$ ) in all of the four analyses depicted in Table I and Figure 1. These form three clusters: in the right pSTS and bilateral MTG/lateral occipital region. See text p. 12–13 for further details. [Color figure can be viewed in the online issue, which is available at [wileyonlinelibrary.com](http://wileyonlinelibrary.com).]

**TABLE V. Non-object and object-related hand movements observation**

Region	Side	X	Y	Z	Z score
Hand > Hand-object					
STS /MTG	R	54	-42	6	2.55
	L	-56	-52	2	2.37
MTG/Lat Occ	R	52	-70	-4	1.94
Occ Pole	L	-18	-100	-4	1.73
SMG (hIP2)	L	-44	-38	44	3.16
Hand-Object > Hand					
Fusiform G.	R	40	-48	-18	2.55
	L	50	-70	10	1.86
Lat Occ G.	L	-42	-72	2	1.99
	R	38	-34	58	2.84
SPL	L	-24	-60	56	2.76
	L	-40	-44	58	1.91
SPL/Postcentral	L	-62	-22	36	2.14
S. Prec./SFS	R	32	0	58	2.28
	L	-22	-6	60	3.09
I. Prec	R	46	8	34	2.29
	L	-56	6	30	2.88
Cerebellum	R	14	-78	-46	1.84

Regions with significant ( $P < 0.05$ ) differences between the two conditions.

intraparietal sulcus (overlapping with caudal part of BA2), temporo-occipital cortex (overlapping with V5), and right fusiform cortex (see Table V). Higher convergence for

intransitive than object-directed hand movements was found in the SMG and posterior STS regions.

### Modulation By Task Demand

To identify differences in activation pattern that may relate to the attentional demand in individual experimental designs, we contrasted experiments that used an explicit task with those that used passive observation. For face movements, explicit attention was associated with significantly higher convergence in the right fusiform cortex, right STS, and medial prefrontal cortex. The reverse contrast showed higher convergence for passive observation in a small cluster within the ventral premotor cortex. When considering the body movement category, a modulation by task demand was seen in right supramarginal gyrus (SMG, area hIP2) and left intraparietal sulcus (area BA 2 and hIP1). The reverse contrast (higher convergence for passively observation) revealed results bilaterally in the lateral occipital/inferior temporal sulcus. Hand movement observation showed a positive effect of task in two small clusters: one in the left inferior temporal sulcus and one in the right posterior parietal cortex. Conversely, higher convergence for passive observation of hand movements was observed in a bilateral region between the posterior STS and supramarginal gyrus.

Interestingly, the regions identified by the conjunction analysis of the main effects did not overlap with these

**TABLE VI. Studies entered into the meta-analyses of static stimuli**

Ref.	Meth.	N	Stimuli	Task
<b>Faces</b>				
Bird	fMRI 1.5	16	Faces > Houses	Passive viewing
Benuzzi, 2007	fMRI 3T	24	Faces or faces parts > mosaic pattern	Gender decision
Blonder	fMRI 1.5T	14	Faces > House	Passive viewing
Gorno-Tempini, 1998	PET	6	Faces > scrambled images	Same-different decision
Haxby, 1999	fMRI	5	Faces > Houses	Match-to-sample task
Holt, 2006	fMRI 1.5T	16	Faces > Blank	Passive viewing
Ishai, 2005	fMRI	12	Faces > scrambled images	
Keslwer-West, 2001	fMRI 1.5T	21	Faces > scrambled images	Concentrate on expression
Kitada, 2009	fMRI 3T	16	Faces > Objects	Identification
Kowatari, 2004	fMRI	12	Familiar faces > Blank	Decide identity
Pierce, 2004	fMRI 1.5T	10	Faces > Blank	Passive viewing
Pinsk, 2009	fMRI 3T	10	Faces > Objects	Fixation task
Platek, 2006	fMRI 3T	12	Faces > Scrambled images	Decide known/unknown
Pourtois, 2005	fMRI 1.5T	13	Faces > Houses	Gender categorization
Willems, 2010	fMRI 3T	16	Faces > Chairs	Monitor (rare) repetition of stimulus
Wright, 2006	fMRI 1.5T	12	Faces > scrambled images	Identity matching
<b>Body or body parts</b>				
Bracci, 2010	fMRI 3T	15	Body parts > Objects	One-back task
Hodzic, 2009	fMRI 3T	10	Body > Object	
Hodzic, 2009	fMRI 3T	16	Body > Object	
Kitada, 2009	fMRI 3T	16	Hand or foot > Object	Identification
Pinsk, 2009	fMRI 3T	10	Hand or Foot > Object	Fixation task
Willems, 2010	fMRI 3T	16	Body > Chairs	Monitoring

Meth = method: fMRI field strength or PET; N = number of subjects.

**TABLE VII. Regions of significant ALE scores for static faces (16 experiments) and static body perception (six experiments; Same labels as for Table III)**

Region	Side	X	Y	Z	ALE score	Z score
<b>Static body perception</b>						
Lat. Occ./Inf. Temp. G	R	48	-70	-6	21.91	5.50
	R	48	-64	-10	10.41	3.94
	L	-46	-78	-2	9.70	3.84
Lat. Occ./MTG	R	50	-66	4	18.36	5.65
	L	-48	-66	2	15.52	5.13
Fusiform G.	R	42	-42	-16	8.00	3.5
	L	-40	-42	-18	11.21	4.1
SPL	R	36	-44	56	8.50	3.6
IPS	R	36	-50	40	9.50	3.77
<b>Static face perception</b>						
Lat Occ	R	42	-78	-8	19.75	4.94
	R	52	-74	0	17.82	4.6
	L	-40	-82	-8	21.4	5.21
Occ Pole	R	26	-100	2	11.15	3.36
	L	-14	-98	-4	14.36	4.00
MTG/pSTS/SMG	R	52	-44	8	23.32	5.51
Angular G.	R	52	-46	18	18.09	4.65
	L	-56	-58	36	13.88	3.9
SPL	R	28	-52	42	11.65	3.45
Post cingulate	R	4	-58	28	20.57	5.08
IFG (BA45)	R	52	24	26	21.17	5.26
	L	-46	20	22	13.99	3.92
pre-SMA	R	0	20	54	15.85	4.28
MFG (BA44)	R	42	12	30	20.41	5.05
	R	12	52	16	17.36	4.54
Medial PF	R	8	46	36	13.89	3.9
SFG	R	14	28	50	15.72	4.25
	L	-24	24	42	15.72	4.25
	L	-24	34	42	15.72	4.25
S. Prec	R	36	2	42	13.89	3.9
Amygdala	R	20	-8	-14	33.84	7.06
	L	-16	-6	-12	23.32	5.51

task-modulated regions and there was no overlap between the regions showing attentional modulation for the different categories.

## DISCUSSION

The current meta-analysis provides a quantitative synthesis of brain imaging studies that have investigated human movement perception, allowing us to generalize results from individual studies to a much larger population (184–291 subjects included in experiments pertaining to the different categories, with a total of 993).

We found that occipito-temporal, premotor, and parietal areas were significantly activated for observing all forms of biological motion (though to differing extents), and exhibited a coarse topographical organisation. We also observed different maxima for transitive and intransitive hand movements. Finally, we identified two regions, one in the posterior STS, one at the junction between the middle temporal and lateral occipital gyri that showed conver-

gent activity in all the movements observation conditions, independently of task demand. We discuss the main regions that were consistently activated by all stimuli or specifically for a single class of stimuli.

### Shared Neural Regions for All Biological Motion

The meta-analysis data show that perception of human movement conveyed by the face, body, and hands all reliably recruit a bilateral temporo-occipital region at the level of the transverse occipital sulcus and a more dorsal and anterior region in the right posterior part of the STS.

The first of these regions overlaps with the structurally and cytoarchitectonically defined area MT/V5 [Dumoulin et al., 2000; Malikovc et al., 2007; Wilms et al., 2005] and is not modulated by task demand. Further, our data indicates that activity here is driven by the perception of human movement above both non-human movement and non-moving human stimuli: convergence in this region

TABLE VIII. Additional sub-analyses

Region	Side	X	Y	Z	ALE score	Z score
Moving hand > Static hand (11 experiments)						
Lat. Occ./Inf. Temp. G/MTG	R	46	-64	0	19.37	5.28
	L	-46	-68	4	18.45	5.54
pSTG	L	-58	-52	10	12.31	4.03
SPL	R	34	-46	60	13.59	4.84
	L	-32	-48	60	13.05	4.07
SPL/IPS	R	38	-38	44	8.05	3.09
	L	-38	-40	44	14.23	4.47
Post SPL	R	24	-84	32	14.45	4.54
	L	-20	-86	32	15.54	4.45
Moving faces > Static faces (14 experiments)						
Middle Occ. G.	R	24	-90	0	8.77	3.19
	L	-26	-98	-4	11.62	3.85
MTG/Lat Occ. G.	R	46	-72	0	18.96	5.32
	L	-46	-70	-4	20.32	5.56
MTG	R	52	-60	4	20.53	5.59
pSTS	R	60	-34	10	15.78	4.72
	R	56	-48	4	21.15	5.73
	L	-50	-50	6	18.07	5.16
Mid STS	L	-56	-16	8	10.97	3.72
S. Prec.	R	46	0	46	14.93	4.54
I. Prec.	L	-42	10	26	15.70	4.70
IFG	R	56	12	16	12.28	4.00
	R	60	24	20	12.74	4.08
Medial PF	R	2	22	46	9.33	3.30
Human movement > Non-human movement (21 experiments)						
Lat. Occ./Inf. Temporal G	R	50	-68	-2	30.47	6.14
	L	-44	-74	2	19.54	4.5
MTG/pSTS	R	54	-54	10	37.10	7.02
	L	-52	-50	4	25.48	5.43
Mid STS	R	52	-16	-18	13.10	3.38
Fusiform	R	42	-54	-20	22.86	5.1
	L	-40	-48	-20	18.42	4.35
Amygdala	R	22	-8	-18	16.29	3.97
Postcentral	R	38	-32	60	14.11	3.48
SMG	L	-54	-28	38	15.18	3.78
S. Prec	L	-26	-4	62	15.41	3.81
I. Prec	L	-50	8	28	16.86	4.07
IFG	R	52	22	24	13.96	3.55
	L	-48	20	18	14.29	3.61

was also significant in the meta-analyses contrasting human motion to non-biological motion, as well as in the contrasts between human movement and static human shape perception. This region overlaps partially with the region of maximal convergence identified in the meta-analysis of experiments related to static body or body parts perception that likely corresponds to the EBA [Downing et al., 2000]. Indeed, most experiments on body perception report some overlap between EBA and MT/V5 [review in Peelen, 2007]. However, two recent studies using multivariate pattern classification have convincingly demonstrated that distinct neuronal populations exist in this area responding to non-specific movement and to body shape perception, respectively [Downing et al., 2007; Peelen et al., 2006]. This latter study led the authors to conclude

that activation by biological motion seen in regions specific to body perception is due to the mere presence of a body shape. Our results, albeit based on only six experiments about static bodies, indicate however, that the EBA is only partially overlapping with the region activated by moving stimuli and thus that within the MT/V5 complex, there may exist a region adjacent to the EBA, that is responsive to all, face, body, and hand movements. This is consistent with studies using point-of light displays that have shown no overlap between biological motion perception, motion and shape perception [Servos et al., 2002]. Further experiments are needed to further characterize this area.

The posterior STS (pSTS) has mainly been emphasized in experiments on biological motion perception using point-light displays, often revealing a right hemispheric

bias [Brancucci et al., 2009; Grossman et al., 2000; Pelphrey et al., 2003]. Its involvement has been reported during imagining point-light biological motion displays, when viewing inverted walkers [Grossman and Blake, 2001] or when viewing images of implied motion [Kourtzi and Kanwisher, 2000; Peuskens et al., 2005; Senior et al., 2000]. In addition, individual fMRI analyses have evidenced overlap of activation in this location for the perception of hand and face movements [75% of subjects in Grosbras and Paus, 2006] as well as for face, leg, and hand movements [33% of subjects in Wheaton et al., 2004] or for face and finger movements [64% of subjects in Thompson et al., 2007]. Group studies reported highly similar coordinates for the centre of overlap between the different human movement observation conditions [Grosbras and Paus, 2006; Thompson et al., 2007]. Thus, our results, which pool the presently available literature on movement observation, confirm observations in individual studies and further stresses the role of the right pSTS in human movement observation.

This region has not been reported in studies focused on static body or body parts perception, as evidenced by our meta-analysis of this topic. This suggests that the pSTS is involved in extracting specific human body movement patterns rather than bodily shape. This is consistent with Beauchamp et al. [2003] report of higher activity in the exact same location when subjects watched articulated motion with many degree of freedoms as compared with artificial unarticulated motion. This pSTS region, also showed significant convergence for static faces perception. This might be due to implied motion often conveyed by faces stimuli. The overlap with the region revealed by the conjunction analysis was minor, however, reinforcing the argument that there exists a region whose activity is specific for socially valenced motion perception.

Note that this region is distinct from the region of the temporo-parietal junction that has been highlighted in a number of studies of theory of mind or perspective taking [Decety et al., 2002; Van Overwalle, 2009]. Also, its activation does not seem to depend upon the task. Therefore, we think that this region is more closely related to socially valenced motion perception than to higher level inferences. It may correspond to the region in non-human primates where single cell recordings have shown neurons selectively responding to various biological actions such as walking, turning of the head, bending of the torso, moving of the arms, facial movements, or object-directed hand movements [Jellema and Perrett, 2002]. This region receives convergent information from the dorsal visual stream via MT and MST as well as from the ventral stream via IT and is connected with the inferior parietal cortex [Seltzer and Pandya, 1994]. Therefore, it is well placed to integrate information from regions with category-specific neuronal responses and to form a complex, high-level representation of human movement. Further experiments are needed to explore the specificity of the pSTS and its integration with the middle temporal/lateral occipital region that also showed convergence for all movements' condition, as

well as with the other nodes of the action observation circuit.

### Topological Representation in STS/STG

Besides this common activation across the different categories of human movement observation, several adjacent regions showed reliable activation for two or one conditions only. The earlier review of Allison et al. [2000] suggested that body movement perception is represented in a more posterior region of the STS/STG than are face (mouth and gaze) and hand movements. Individual studies, using single-subject or group analyses, provided some mixed support for this. Pelphrey and colleagues [2005] reported that hand movements elicited more ventral activity than eye movements, while watching mouth movements engaged more anterior regions in the middle part of the STS. But their study only examined dominant activity (i.e., eye-ctr > hand-ctr) and did not consider overlaps. Wheaton et al. [2004] reported more posterior and medial activation within the STS for leg than face movements, but the figures do not suggest a clear spatial segregation. Also, in their study no activity was observed during hand movement observation. Thompson [2007] reported common activation to hand and face motion in the right posterior part of the STS and concluded that this region is not body-part specific.

Our meta-analysis showed besides the area of convergence, an approximate somatotopy which is roughly paralleled in both hemispheres. In general, it seems that representations conform to an organization in which computation on body stimuli occurs in more superior, posterior regions, followed by hand and descending inferiorly and more anteriorly to face regions. This is in line with the proposal that the STS is closely related to the mirror neuron network [Keysers and Perrett, 2004; Montgomery and Haxby, 2008] and the fact that visual response in the STS is suppressed during action execution as reported in monkey single-cell recording [Hietanen and Perrett, 1993] and fMRI [Kontaris et al., 2009; Leube et al., 2003]. Thus, the STS/STG region might be a locus of interaction between complex visual representation of human movement and efference copies of voluntary action [Iacoboni, 2001]. The extension of activity related to different effectors into different territories adjacent to the STS is perhaps related to the use of the information for different purposes (e.g., face movement for communication, hand to recognize intention), which could be reflected in such a modular organization.

Of particular interest is the large overlap between the activity during watching gaze movements and watching hand conditions. This is in tune with the idea that these social stimuli convey information that resonates with each other in referring to the environment.

The fact that the meta-analysis did not identify significant convergence in more anterior regions along the STS might reflect a lack of consistency between studies. It

might, however, also relate to anatomical variability in STS [Ochiai et al., 2004], yielding different standardized coordinates for regions in the mid-STS that might be equivalent. Also, in many studies, a large part of STS can be activated, constituting a single cluster, whereas only a single maximum is reported. This might bias the results towards more posterior regions, where the activity might be higher.

Finally, the site of convergent activation in the middle STS region for the face condition only is very close to the voice areas [Belin et al., 2000]. This suggests that observing visual signals that can be associated with vocalization recruit the same regions as listening to the corresponding signal. This is also in line with the idea that anterior regions of the STS might be recruited for social signals linked to communication.

### Fronto-Parietal Regions

Reliable activations in the frontal lobe also exhibited some rough somatotopical organisation for hand (object and non-object related) and face movement observation. Although the results from the two categories are overlapping, face movement observation yielded clusters more ventral and rostral than hand movement within cytoarchitecturally defined BA44. Such organization speaks in favor of BA 44 as the human homolog of macaque area F5 where (effector-specific) mirror neurons were discovered using electrophysiological recordings [e.g., DiPelligrino et al., 2005; Gallese et al., 1996]. Our meta-analysis thus confirms and extends the conclusion made in individual studies about the organisation of human mirror areas and the direct matching between observed and planned actions [Buccino et al., 2004; Gazzola et al., 2006; Rizzolatti and Craighero, 2004]. We did not observe significant convergence for body perception, despite some reports in individual studies, potentially due to lack of power or due to anatomical disparity in the recruited region [Keller et al., 2009].

The other region where mirror neurons were observed in monkeys, namely the anterior parietal cortex, showed significant convergence for hand and body (with again a crude topographical organization) but not face movements observation. This points towards different sensitivity for different effectors in the different nodes of this action observation and matching system.

Convergence between object-related hand movements and face observation was seen in a region of the right superior precentral sulcus that corresponds to the dorsal premotor cortex. Interestingly, only studies of eye movement observation contributed to the face clusters. This is consistent with our previous meta-analysis of eye-gaze perception which showed convergent activation during overt and covert shifts of attention as well as during gaze perception [Grosbras et al., 2005]. Moreover, this brain location is also consistently involved in the manual movements in response to simple cues [Chouinard and Paus,

2006], stimulus-driven reorienting [Cieslik et al., 2010] as well as in visually guided grasping [Davare et al., 2006; Wise et al., 1997]. Recent evidence indicates a sensitivity to the ultimate goal of an action, regardless of the transmitting effector [Majdandzic et al., 2009; Shubotz et al., 2008]. Hand and eye information exhibit a highly coordinated relationship, maybe sharing a common neural mechanism according to task demands [Neggers and Bekkering, 1999; Thura et al., 2008]. Activation clusters in this meta-analysis on passive observation of biological movement thus allude to preparatory cell activity for implementing reflexive social attention.

The segregation in activation likelihood parting the parietal lobe when watching hand or whole body movements is in keeping with Milner and Goodale's model of visuo-motor programming and control of action [Milner and Goodale, 2006]. They propose a network of modules within the parietal lobe, which mediate the visual guidance of action in terms of the effector system employed. Our results illustrate that an effector-based transformation is maintained under conditions of passive observation.

### Transitive and Intransitive Hand movements

Object-directed hand movements yielded significantly higher convergence in regions that are considered homolog of mirror-neuron regions in the monkey, namely the ventral premotor/inferior frontal gyrus and anterior parietal cortex. Our results are in tune with the fact that mirror neurons are activated primarily by the view of a biological effector and an object; the effector alone or the object alone are often insufficient to trigger any activity [Rizzolatti and Craighero, 2004]. Common activation between action observation and imitation has also been reported in these regions in individual fMRI studies [e.g., Iacoboni, 2009] and in two previous meta-analyses [Caspers et al., 2010; VanOverwalle, 2009] again pointing towards the homology between BA44 and F5. Notably, the differential convergence for intransitive and object-related hand conditions in the anterior parietal cortex matches evidence of "manipulation" cells sensitive to either object properties, appropriate hand/finger postures for the goal, object, or both [e.g., Sakata et al., 1995].

### Comparison with Other Meta-Analyses

Other quantitative analyses have reviewed brain regions involved in social perception. In particular, Caspers et al. [2010] have performed ALE meta-analyses of 104 experiments contrasting action observation to various control conditions and compared them to experiments on action imitation. There is some degree of overlap with the present meta-analysis. But because of different focus (comparison between observation and imitation on the one hand and assessment of different factors involved in action observation on the other hand) our selection criteria were different, resulting in only 31 experiments commonly included in both analyses. These mainly pertained to (transitive or

intransitive) hand movement observation. Although this previous meta-analysis already compared hand movement observation to other categories (mainly to explore possible confounds) their results were much more restricted than our comparative analysis, which includes a much larger corpus of experiments related to body or face observation. Our results confirm and amend the results from this previous meta-analysis in several important aspects: we are able to show common convergence for three categories of effectors in the right posterior STS and in the vicinity of the MT/V5 and EBA complex. We tentatively demonstrate a topographical organisation of the representation of body, hand, and face movements in the temporal and fusiform cortex, for body and hand in the parietal cortex and for hand and face in the inferior frontal cortex. Moreover, by segregating studies according to the nature of the control condition and comparing the meta-analyses on human movement observation to that on static human stimuli we are able to draw conclusions related to the sensitivity of different regions to human movement above non-specific movement and human shape perception.

## CONCLUSION

The present meta-analysis provides a landmark summary to guide future brain imaging experiments on social perception and inform brain stimulation studies. The findings support a model of automatic engagement of category specific regions in the temporal cortex as well as in frontoparietal regions when observing human movement. Besides, we demonstrated convergent processing of all categories in the posterior STS and lateral occipital cortex, maybe mediating integration of information provided by different kind of bodily movement.

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