

Predicting the actions of others taps into one's own somatosensory representations—A functional MRI study

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Abstract

Humans have the striking capacity to predict actions performed by their conspecifics. But how exactly do we perform such predictions? Do we use our own action repertoire and our own body to simulate the reaching range of others? In this functional magnetic resonance imaging study static photographs depicting side views of seated human models were presented to participants, who had to predict whether the models could reach a target placed in front of them. The predictions were performed both fast and accurate, but with an overestimation bias as well as higher error rates and slower predictions for targets close to the models' actual reaching ranges. Specific hemodynamic signal changes were detected in primary and secondary somatosensory cortices, inferior and superior parietal areas, and in right ventral premotor cortex. These findings demonstrate that action prediction in the current context activates a network of areas involved in action recognition, visuo-spatial transformation and somatosensory anticipation. The results are in line with the mirror-neuron system account of action understanding and the notion of the common coding theory that actions are coded in terms of their perceivable effects.

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Keywords: Action prediction; Common coding theory; Mirror-neuron system; Motor cognition; Simulation; Somatosensory cortex

1. Introduction

An increasing number of behavioral and functional imaging studies indicates that mental representations are grounded in sensorimotor interactions with the physical environment (e.g., Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005; Sommerville & Decety, 2006). These representations subserve both action understanding and action production by supporting internal simulations of these behaviors (see Jackson & Decety, 2004; Wilson & Knoblich, 2005, for recent reviews). An influential conceptual framework for understanding these shared representations and the link between perception and action is provided by the common coding theory (Prinz, 2003). This theory claims that somewhere in the chain of operations that lead from perception to action, derivatives of

sensory stimulation and certain antecedents of action effects are generated that are commensurate in the sense that they share the same system of representational dimensions (Hommel, Müssele, Aschersleben, & Prinz, 1998; Knoblich & Prinz, 2005). The core assumption of common coding is that actions are coded in terms of their anticipated effects, i.e., the distal perceptual events they should generate. Performing a movement leaves behind a bidirectional association between the motor pattern it was generated by and the sensory effects it produces. Such an association can then be used to retrieve a movement by anticipating its effects (Heyes, 2005; Hommel, 2004). These common perception/action codes are also accessible during action observation, and perception activates action representations to the degree that perceived and represented actions are similar (see also Sommerville & Decety, 2006).

Direct support for a functional and neurophysiological overlap of perceptual and action-related codes has been provided by the discovery of mirror neurons. Mirror neurons discharge both during the performance of goal-directed actions and the perception of actions made by others. In this sense, they are

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perspective-independent. Mirror neurons have been identified in the ventral premotor and posterior parietal cortices of monkeys (see Fadiga & Craighero, 2004; Rizzolatti & Craighero, 2004, for review). A large number of functional neuroimaging studies with humans documented the selective recruitment of homologous cortical regions that implement action representation in premotor and parietal cortices during the mere observation of others' actions (see Blakemore & Frith, 2005 for review). This mechanism may subserve different functions, including action understanding and action prediction.

One interesting way to test whether we use our own motor representations to understand and predict the behavior of our conspecifics is by asking participants to estimate the reaching range of other individuals. A series of behavioral studies conducted by Fischer (2003, 2005a) explored how participants accomplish this task. In these studies, observers predicted whether a model would be able to reach an object that was placed at various distances within (e.g., very near or near targets) or outside of (e.g., far or very far targets) the model's true reaching range. Three main findings were obtained. First, the speed with which predictions were made showed an inverted relationship with target distance, with targets that were very far or very near leading to faster decisions, compared to near and far targets. This indicates that the task became harder as targets were positioned closer to the model's true reaching range. Second, the accuracy of ratings was biased towards overestimating the range of the model, much as for reaching range evaluations for oneself (Fischer, 2000, 2005b). Thus, targets that were outside of the model's true reaching range were sometimes perceived as reachable. And finally, observer postures (upright or bent) had no effect on the speed or accuracy of responses about the reaching range of a model displayed in congruent or incongruent postures (Fischer, 2005a). However, observers' decisions were faster and more accurate when the observed model would have had to perform fewer postural changes to adopt the to-be-evaluated reaching posture. This latter result replicates previous findings in the motor imagery literature (e.g., Johnson, 2000; Parsons, 2003) and rules out a mere visual estimation process as the underlying solution strategy—because a strategy exclusively based upon visual imagery would not be sensitive to the complexity of the required movements.

However, the precise nature of the motor simulation involved in reachability estimation for others remains unclear from these behavioral results. Participants may have performed a first-person motor simulation, taking into account their own body schema to decide whether the model can reach the target. Alternatively, they may have relied on the mirror mechanism described above, and an automatic mapping from perception onto action simulation. Automatic mapping in this case refers to a process that enables a transition from perceptual to action representations that is non-intentional, unaware, efficient and non-controllable by the observer (Bargh, 1994). The present study explored these possibilities by using functional magnetic resonance imaging (fMRI). Specifically, we investigated which sensorimotor representations are activated when individuals are requested to predict the reaching range of others. The following hypotheses were tested by our study:

- (1) If predicting the reaching range of others involves motor simulation from a first-person perspective, it should recruit areas that would be involved in performing the action that participants have to simulate. These areas predominantly include dorsal lateral premotor areas, supplementary motor area, posterior parietal areas, and the cerebellum. In addition, activation in ventral premotor cortex and possibly also in primary motor cortices would be expected. It has indeed been demonstrated that mental simulation of action by means of motor imagery recruits neural networks that are considerably overlapping with those involved in the actual performance of those actions (e.g., Decety & Grèzes, 1999; Ehrsson, Geyer, & Naito, 2003; Michelon, Vettel, & Zacks, 2006; Naito et al., 2002; Roth et al., 1996; Ruby & Decety, 2001). For reaching movements, dorsal premotor cortex seems to play a special role as neurons in this area integrate information about the target to be reached and the body part and action to reach it (Cisek & Kalaska, 2005; Hoshi & Tanji, 2000).
- (2) If predicting the action capacities of others taps into the mirror-neuron system, one should detect signal increases in key areas of the human mirror system, specifically the inferior frontal gyrus and inferior–posterior parietal cortex, as well as the posterior superior temporal sulcus in which neurons are sensitive to the sight of actions made by others (Kable & Chatterjee, 2006; Puce & Perrett, 2003). There is strong evidence that the inferior frontal gyrus (the human homologue region of monkey F5 area) plays a crucial role in action understanding. For example, a recent fMRI study in monkeys shows selective recruitment of subregions in monkey ventral and dorsal premotor regions depending upon the observed action (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005). Recently, Pobric and Hamilton (2006) demonstrated selective impairment of a perceptual weight-judgment task when repetitive transcranial magnetic stimulation (rTMS) was applied over the left inferior frontal gyrus. Similarly, Grèzes, Frith, & Passingham (2004) reported right inferior frontal gyrus activation when participants judged individuals lifting boxes of different weights. Altogether, these studies provide evidence for the role of this region in action recognition and action understanding. Note also that activation in the mirror neuron circuitry, and in particular in the inferior parietal cortex, would be predicted by the goal-directed nature of the reaching predictions, as the activity of mirror neurons in this part of the cortex is specifically modulated by whether an observed action is or is not object-directed (e.g., Fogassi et al., 2005; Umiltà et al., 2001).

A more detailed understanding of the neural mechanisms underlying our predictions of other peoples' reaching ranges can be achieved by manipulating the effector involved in the prediction task. If our decision about reachability of a target is based on the imagined movement of a particular effector, then we would predict somatotopic activation patterns in primary motor and premotor areas of the brain—as might be inferred from some recent findings of somatotopy during motor imagery

and action observation (e.g., Buccino et al., 2001; Ehrsson et al., 2003; Michelon et al., 2006). Such a result would be in line with motor simulation from a first-person perspective.

Alternatively, a lack of somatotopic activation would be in harmony with the perspective-independent and goal-oriented nature of the mirror mechanism. It implies the engagement of more abstract representations and an anticipation of action goals, as is also assumed under the common coding framework. This framework emphasizes the representation of ends over means and its implementation would not require a coding of the detailed muscular or sensory activation patterns involved in a goal-directed reaching action. To test these predictions, we asked our participants to estimate, in separate task conditions, the reaching range of another person's hand or foot. The cortical control of these body parts is spatially distinct, with more dorso-medial activation of contralateral motor areas for leg compared to arm movements, respectively.

2. Material and methods

2.1. Participants

Seventeen right-handed (Annett, 1985) healthy volunteers (nine females) aged between 18 and 35 years (mean = 24.88 years, S.D. = 4.83) participated in this study. They gave informed written consent and were paid for their participation. No subject had any history of neurological, major medical, or psychiatric disorder. The study was approved by the local Ethics Committee (Centre Léon-Bérard, Lyon, France), and conducted in accordance with the Declaration of Helsinki.

2.2. Task and stimulus description

The two main experimental conditions in this study were predicting the reaching range of a model's hand or foot from static photographs. Note that static pictures are sufficient to activate the mirror-neuron system (e.g., Cheng, Meltzoff & Decety, 2006; Nishitani & Hari, 2002; Stürmer, Aschersleben, & Prinz, 2000; Urgesi, Moro, Candidi, & Aglioti, 2006). Participants had to evaluate whether a human model could reach (i.e., touch) a target placed in front of him/her by extending either his/her hand or his/her foot in a specific way (Fig. 1). The way in which the model could move to reach the targets was explained by verbal instructions as well as by the experimenter demonstrating the reaching

movements. Targets were placed at four different distances from the model, similar to Fischer's (2005a) original method. In addition, two control conditions – fixation and gender matching – were implemented. Fixation of a green dot placed on the same grey homogeneous image background as the model photographs served as a baseline control condition. In the gender matching condition, participants decided whether the gender of the photographed model matched with a gender symbol (σ or φ) placed at one of the four target positions used in the experimental conditions. The aim of this condition was to control for various high- and low-level processes such as response preparation and execution, goal-directed eye movements, and, most importantly, a detailed visual-spatial analysis of the model's body shape and proportions.

For the task stimuli, 10 models (5 females) sitting on a chair with back support were photographed from their left side. All models wore identical sleeveless shirts and shorts that clearly revealed their arms and legs. Photographs were taken from a distance of 320 cm between camera lens and model. Each model was photographed three times: (1) in a standard posture sitting with upright back, arms and hands vertically extended, both legs next to the chair, and the ankle joint extended, as if standing on their toes (Fig. 1); (2) in the same posture but with the left leg and foot maximally extended forward; (3) leaning forward on the chair, with torso, arms and hands maximally extended forward while keeping shoulders, arms and hands parallel. The second and third photographs provided the maximum foot and hand reaching ranges. This information (which was never available to participants) was used to edit the standard posture photograph of each model as follows: First, for each range separately, the horizontal distance between maximum range and the nearest surface of the effector with that range was measured. Next, a single vertical bar marker was drawn into each photograph with the surface facing the model located $\pm 30\%$ or $\pm 10\%$ from that model's maximum range. These four marker positions represented the very far (+30%), very near (–30%), far (+10%) and near (–10%) targets, respectively. For the gender matching task, male and female gender symbols (σ or φ) were placed at the same positions. In order to avoid implicit evaluations of reaching range in the gender matching task, models were flipped so that their back faced the symbols. Gaze perception is known to have a modulatory effect on mirror neuron activity (Jellema, Baker, & Perrett, 2000). Therefore the head of the model was rendered unrecognizable by applying a mosaic pixelation filter, removing identity, gender and gaze direction information from the head region. In addition to using the original photographs taken from the left side of the model, all photographs were digitally flipped around their vertical axis. This generated pictures in which the model was positioned on the left side of the photograph and in which its body was seen from the right side. In a behavioral pre-test with nine different participants, the stimuli generated using the 10 different models were validated. This pre-test basically replicated previous studies using similar reaching range estimates (Fischer, 2005a) and established that both reachability and gender matching decisions were made within around 1 s on average. Also, homogeneous results in terms of task difficulty and reaction times were obtained for the different models



Fig. 1. Examples of the stimuli shown in the hand reaching condition (right) and the foot reaching condition (left). Both targets are placed at far distances, i.e. 10% beyond the true reaching ranges of the shown model.

and for both the flipped and original pictures; thus all 80 available stimuli were used in the fMRI study.

2.3. Behavioral data and analysis

Two imagery questionnaires (Hall & Pongrac, 1983; Sheehan, 1967) were filled out by participants, assessing individual differences in visual and motor imagery abilities. In order to reduce social desirability and study-compliant responding, questionnaires were completed without information about the purpose of the study, and were filled in several days before the fMRI experiment. After scanning, individual task solving strategies were assessed using an exit questionnaire. The exit questionnaire assessed whether participants adopted the perspective of the model, using motor imagery to reach the target in their imagination—or whether they used an allocentric/observational third-person perspective, employing visual imagery to imagine how the model reaches out to the target. An example question for the first strategy is “Did you imagine yourself being in place of the person [on the photo], moving your torso and arms to reach the target placed in front of you”; for the second strategy, questions like “Did you imagine the person [on the photo] moving his/her torso and arms to attain the target placed in front of him/her?” were asked.

During the experiment, response times (defined as the time intervals from onset of a picture to pressing of a response button) and accuracy data were collected using a button box connected to the stimulus presentation software. Response times and accuracy data were analyzed using repeated measures analyses of variance with factors effector (two levels: hand or foot) and target distance (four levels: very far, far, near, very near), and *a priori* contrasts of factor levels. Violations of the sphericity assumption were considered by correcting degrees of freedom according to Greenhouse–Geisser, and by computing contrasts with specific error-variances (Boik, 1981).

2.4. fMRI paradigm

Although a great deal of knowledge is available concerning the neural networks involved in action understanding and action perception, this study represents the first one in which brain activation during reaching range evaluations was investigated using functional neuroimaging. Thus, our main aim was to obtain measurements of the hemodynamic responses with optimal detection (i.e., localization) power. We therefore employed a blocked stimulus presentation and data acquisition mode, with block durations being closely matched to the fundamental frequency of the hemodynamic response function to optimize the detection of task-related hemodynamic responses (Friston, Zarahn, Josephs, Henson, & Dale, 1999; Henson, 2003). Each block consisted of an instruction screen and nine different photographs of one condition (hand or foot reaching, or gender matching). Each task item was presented for a maximum duration of 2100 ms, and a blank grey screen was presented for a duration of 200 ms upon button press. The screen position of stimuli was jittered to avoid the possibility that subsequent stimuli could be evaluated based upon after-images or screen position memories. Each block was assigned a total duration of 6 repetition times/TRs (i.e., approximately 24 s). In case participants responded before the allotted 2100 ms, a red fixation dot was presented for the cumulative time difference until the end of a block. However, the actual block duration was used to set up the regressors modeling task processing. A green fixation dot was presented in the baseline (fixation) condition. To avoid potential confounds from time pressure and to stress accuracy of responses, participants were instructed to enter their responses as accurately as possible, and told that sufficient time was provided to do this (Lamm et al., 2001a). The sequence of blocks was pseudo-randomized and counterbalanced across participants, with no condition being repeated more than once, and with six blocks of each condition being presented in two consecutive runs. Thus, 12 blocks with a total of 108 tasks were run for each condition. As only 80 different photographs were available, 28 from these 80 photographs were randomly selected and repeated once (with the proportion of target distances and genders held constant).

2.5. fMRI data acquisition and analysis

MR imaging was performed using a whole-body 1.5 Tesla Siemens Sonata scanner (Siemens, Erlangen, Germany). Functional images covering the whole

brain (including the cerebellum) were acquired using an echoplanar imaging (EPI) sequence with the following parameters: echo time TE = 60 ms, repetition time TR = 3920 ms, flip angle = 90°, 40 axial slices with 3 mm slice thickness and 0.3 mm gap between slices, in-plane-resolution 3.44 mm × 3.44 mm (64 × 64 matrix, FOV 220 mm × 220 mm). Images were acquired using an ascending interleaved sequence with no temporal gap between consecutive image acquisitions. Two fMRI runs with 175 image acquisitions were performed. The first five scans of each run were used to achieve steady state magnetization conditions and were discarded from analyses.

Stimulus presentation and response collection were performed using the Presentation software (Neurobehavioural Systems™, Albany, CA, USA). Visual stimuli were presented using a back-projection system and subtended a visual angle of 27.8° × 19.12°. Responses were collected using a button box consisting of two buttons that were pressed using the dominant right hand. Image processing was carried out using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK), implemented in MATLAB 6.5 (Mathworks Inc., Sherborn, MA). Preprocessing included slice-timing correction, correction for head motion (realignment to first image volume), normalization to the EPI template provided in SPM2, and smoothing using a 6 mm FWHM isotropic Gaussian kernel. Accuracy of normalization and motion correction were carefully checked for each subject. Following preprocessing, hemodynamic responses were assessed by setting up fixed effects general linear models (GLM) for each subject. Regressors of interest modeling the experimental and control conditions as well as the instruction screens were set up. Regressors were convolved with the canonical hemodynamic response function (hrf) as defined in SPM2. Fixed effects models incorporated a high-pass filter with a frequency cut-off at 128 s. Following model estimation, contrasts were calculated for each subject to assess differences between conditions and between conditions and baseline (fixation). As hand and foot reaching estimations did not lead to substantially different activations (see Section 3), activation in those two conditions was averaged when contrasting them with the gender matching condition. Contrasts involving averaging across the two conditions will be referred to as reaching range/averaged. The resulting contrast images were entered into second-level random effects (rfx) *t*-tests allowing for population inferences based on the 17 participants. Activation differences between conditions and the fixation baseline were interpreted using a threshold of $P = 0.001$ and a spatial extent threshold of $k = 20$ (corrected for multiple comparisons across the whole volume using false discovery rate – FDR; Genovese, Lazar, & Nichols, 2002). The more subtle differences in signal strength between conditions were thresholded using a more liberal threshold of $P = 0.05$ (corrected using FDR) and $k = 10$. Choice of these thresholds was based upon exploratory data analyses, as well as on signal strength and effect size considerations based on the statistical power of the used block design. However, no explicit power analysis could be performed as no former neuroimaging studies using this or a similar task paradigm were available to estimate the expected effects. Anatomic and cytoarchitectonic labeling of activity clusters was performed using SPM-implemented toolboxes (Anatomy Toolbox, v. 1.3b, Eickhoff et al., 2005). Relationships between response accuracy and hemodynamic responses were assessed by correlating parameter estimates of the contrast reaching range/averaged > baseline with percentage correct (averaged for hand and foot reaching tasks). Informed by significant correlations between questionnaire and behavioral data (see Section 3), we also correlated a subscale of the Sheehan (1967) questionnaire with the hemodynamic responses during the reaching task. Correlation analyses were thresholded at $P = 0.001$ (uncorrected), $k = 5$.

3. Results

3.1. Behavioral data

Figs. 2 and 3 show the behavioral data for the hand and foot reaching tasks.¹ Responses were made after about 1 s on average,

¹ Note that the response time and accuracy data of three subjects had to be excluded due to a minor misunderstanding of what represents a correct response, resulting in a very low percentage of correct answers for the reachable targets.

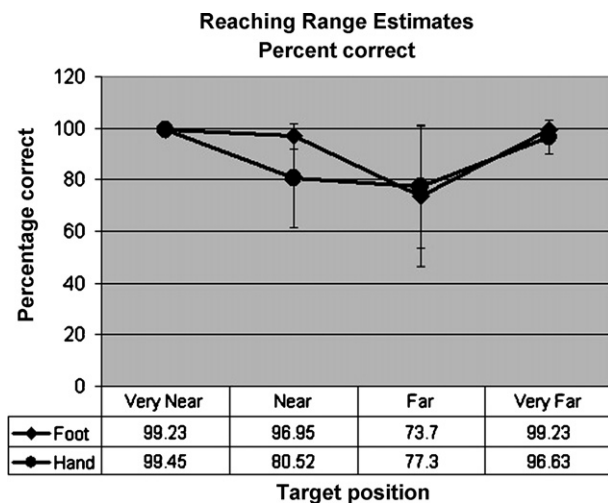


Fig. 2. Average accuracy data (mean \pm S.E.) for the reaching range judgments.

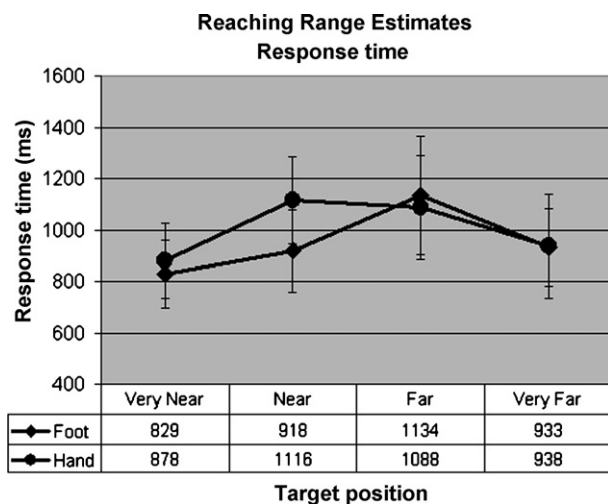


Fig. 3. Average response times (mean \pm S.E.) for the reaching range judgments.

and around 90% of the responses were correct (mean \pm S.D. of percentage correct and response time, averaged across all target distances—foot: 92.26 ± 6.67 , 954 ± 142 ; hand: 88.67 ± 6.35 , 1004 ± 153). Similar values were obtained in the gender matching task (mean \pm S.D. of percentage correct and response time: 89.67 ± 5.99 and 1336 ± 104 ms).

Analysis of variance revealed significant main effects of distance and effector for both response time and accuracy data (main effect of distance for response time: $F(3, 39) = 16.832$, $P < 0.001$, $\varepsilon_{\text{Greenhouse-Geisser}} = 0.522$, effect size $\eta^2 = 0.564$; for accuracy: $F(3, 39) = 10.493$, $P = .004$, $\varepsilon_{\text{GG}} = 0.406$, $\eta^2 = 0.447$; main effect of effector for response time: $F(1, 13) = 15.112$, $P = 0.002$, effect size $\eta^2 = 0.538$; for accuracy: $F(1, 13) = 5.845$, $P = 0.031$, $\eta^2 = 0.310$). The interaction term effector \times distance was significant for response time ($F(3, 39) = 17.999$, $P < 0.001$, $\varepsilon_{\text{Greenhouse-Geisser}} = 0.801$, effect size $\eta^2 = 0.581$), and a trend towards significance was obtained for the accuracy values

($F(3, 39) = 3.685$, $P = 0.055$, $\varepsilon_{\text{Greenhouse-Geisser}} = 0.503$, effect size $\eta^2 = 0.221$).

Both variables showed the familiar relationship with target distance, with very far and very near targets associated with shorter response times and a higher percentage of correct answers compared to near and far targets (planned contrasts for response time, with values of hand and foot conditions being averaged: $F(1, 13) = 92.075$, $P < 0.001$, $\eta^2 = 0.876$; for percentage correct: $F(1, 13) = 45.569$, $P < 0.001$, $\eta^2 = 0.778$). The overestimation bias reported in previous behavioral studies was also confirmed (Fischer, 2005a, 2005b): for targets within reach (near and very near), decision times were shorter than for targets outside a model's reaching range (936 ms versus 1023 ms; planned contrast: $F(1, 13) = 5.094$, $P = 0.042$, $\eta^2 = 0.282$), and the percentage of incorrect responses was higher for the non-reachable compared to reachable targets (13.29 versus 5.96; planned contrast with trend-like significance: $F(1, 13) = 3.161$, $P = 0.099$, $\eta^2 = 0.196$). This effect was mainly due to the difference between near and far targets, as accuracy was nearly identical for very far and very near targets (see Fig. 2).

The post-experimental questionnaires and experimental debriefing indicated that participants did not adopt a first-person perspective when predicting the reaching range of the models. Rather, they claimed to rely upon visual imagery from an allocentric perspective because all except one participant (in the hand reaching condition) reported visually imagining the models moving their respective body parts to reach out to the target. The vividness of imagery was slightly higher in the hand than in the foot reaching condition (mean \pm S.D. ratings: 2.18 ± 0.73 and 1.88 ± 0.78 , respectively; $t(16) = 2.423$, $P = .029$, $\eta^2 = 0.281$, with values ranging from 1 = vague and imprecise visual imagery to 4 = perfectly vivid and clear visual imagery).

The combined analysis of questionnaire and behavioral data revealed a significant negative correlation between the visual imagery subscale of the Sheehan questionnaire and response times (r (Spearman) = -0.573 , $P = 0.02$), but no significant correlations between response times and any motor imagery-related subscales.² Based on this finding, we correlated scores of this subscale with hemodynamic responses during reaching range predictions (versus fixation baseline), with the prediction that they should reveal brain–behavior correlations in (mainly) visual areas. No significant correlations between the subscales of the movement imagery questionnaire (Hall & Pongrac, 1983) and the behavioral data were found ($P > 0.05$ in all cases).

3.2. fMRI data

3.2.1. Reaching range prediction and gender matching versus baseline

Predicting the reaching range of others, averaged across hand and foot tasks, activated a widely distributed neural network that was dominated by activity clusters mainly located in posterior

As subjects still performed the task in the intended manner and showed no abnormalities in their brain activation pattern, their fMRI data were not excluded.

² Interestingly, four out of the five questions asked by the visual imagery subscale required visual imagery of human body parts (e.g., "Imagine precisely the contours of the face, the head, the shoulders and of the body").

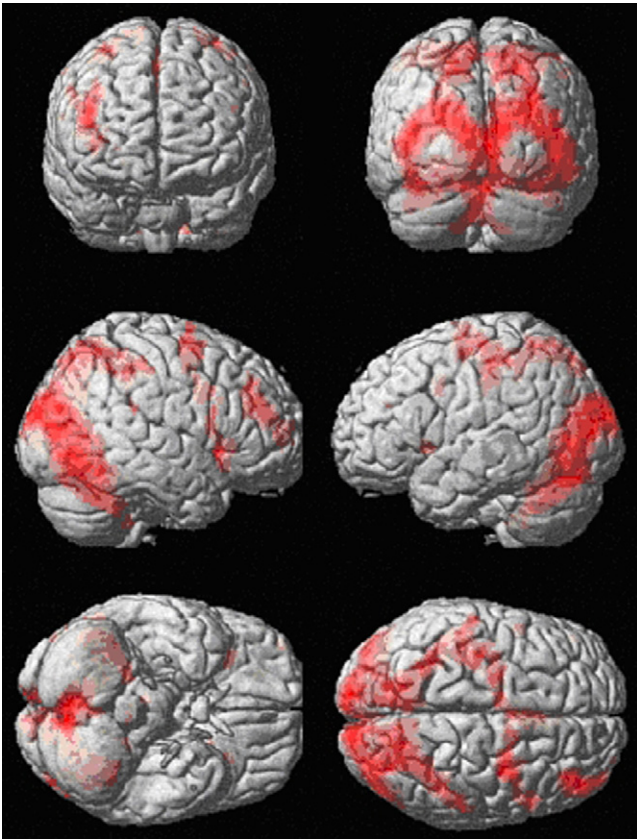


Fig. 4. Significant hemodynamic changes (reaching range/averaged > baseline) resulting from the evaluation of the reaching range of others. Maximum intensity projection of activation, displayed on 3D-renderings of the normalized single-subject structural MRI provided in SPM2 (thresholded at $P = 0.001$, FDR-corrected, $k = 20$).

neocortical areas (Fig. 4). Significant cortical hemodynamic responses were detected in medial (lingual and calcarine sulcus) and lateral portions of occipital cortex (middle occipital cortex, bilaterally), and in bilateral inferior and superior parietal cortex (supramarginal gyrus, superior parietal lobe and precuneus). The large clusters in lateral occipital cortex encompass several brain regions involved in higher-order visual perception and analysis—including the extrastriate body area (EBA). EBA is specialized in the visual analysis of human bodies and body parts and is reliably detected and differentiated from other lateral occipitotemporal regions when using functional localizer tasks (Downing, Jiang, Shuman, & Kanwisher, 2001). Since the main goal of this study was not to localize EBA, we did not perform such a localizer and therefore cannot say with ultimate confidence that what we observed actually is activation of EBA. Significant clusters in left and right postcentral gyrus indicated involvement of the somatosensory cortex. In frontal cortex, activation was found in the supplementary motor area, dorsal medial cingulate cortex, in a cluster comprising left precentral gyrus and left central sulcus, and in a bilateral cluster located at the origin of the superior frontal sulcus that extended into lateral premotor cortex. In more anterior brain areas, significant signal changes were detected in left and right ventral premotor cortex (comprising pars opercularis), in right dorso-lateral prefrontal cortex, and in bilateral anterior insular cortices. In addition to

these cortical activations, substantial hemodynamic changes were detected in medial and lateral regions of the cerebellum (including the vermis), posterior thalamus, in the subiculum, superior colliculi and dorsal pons.

Activation in the gender matching control task (contrast gender matching > fixation) was also dominated by posterior activation clusters in primary and higher-order visual areas, such as medial and lateral occipital cortex (also including EBA), and inferior and superior parietal cortex (precuneus and supramarginal gyrus). In the left hemisphere, an activation cluster partially extended into the somatosensory cortex. In frontal areas, activation was found in bilateral premotor and left primary motor cortex, in medial premotor areas (SMA), dorsal medial cingulate cortex, anterior right middle frontal gyrus, and in the bilateral insula. An activation cluster in right middle frontal gyrus partially extended into the right ventral premotor cortex/pars opercularis.

3.2.2. Reaching range prediction versus gender matching

The target analysis of this study was the contrast between reaching range prediction/averaged and the gender matching control task. This contrast directly assessed the differences between the reaching range evaluations and the gender matching condition, controlling for activation associated with more general processes such as response preparation, movement execution, and visual-spatial analysis of the models' bodies. The contrast revealed stronger hemodynamic responses in bilateral postcentral gyrus and parietal operculum, right superior parietal lobule and inferior parietal cortex, middle occipital gyrus, two clusters in posterior middle cingulate gyrus, and in right ventral premotor cortex (pars opercularis, see Table 1 and Fig. 5). Cytoarchitectonic probability maps suggest that the activation difference in and around right postcentral gyrus was comprising primary somatosensory cortex (SI, Areas 1 and 2) as well as secondary somatosensory cortex (SII, Areas OP1 and OP4; Eickhoff et al., 2005; Eickhoff, Amunts, Mohlberg, & Zilles, 2006; Eickhoff, Schleicher, Zilles, & Amunts, 2006). The clusters in the left hemisphere were generally smaller and only partially extended into primary somatosensory cortex (cytoarchitectonic Area 2). In addition to a cluster in the parietal operculum (SII, Area OP1) that was homologous to the cluster in the right hemisphere, activation was also detected in a more rostral part of left SII (Area OP4, partially extending into Area 3b). One of the two clusters in middle cingulate gyrus partially extended into paramedian primary motor cortex (M1). However, the majority of voxels as well as the center of this cluster were clearly located outside of M1. Notably, no significant activation difference was found in medial or dorso-lateral premotor areas.

The reverse contrast (gender matching > reaching range prediction/averaged) revealed stronger activation in visual areas of medial and lateral occipital cortex, as well as in the precuneus, the superior colliculi, posterior thalamus, cerebellum, hippocampus, medial cingulate cortex, and in bilateral dorso-lateral frontal cortex. In the left hemisphere, activation in the latter was clearly located within Areas 44 and 45. In contrast, the right-hemispheric activation was mostly anterior and medial to the cytoarchitectonic probability maps delineating Areas 44 and 45.

Table 1
Stronger hemodynamic responses during reaching range predictions than during the gender matching control condition (contrast reaching range prediction/averaged > gender matching)

Anatomical location	L/R/M	<i>t</i> -Value	MNI coordinates		
			<i>x</i>	<i>y</i>	<i>z</i>
Parietal Lobe					
Postcentral Gyrus	R	9.42	56	−26	50
x Supramarginal Gyrus	R	6.60	62	−24	36
x Supramarginal Gyrus	R	6.22	60	−26	26
Postcentral Gyrus	R	5.63	32	−38	42
Postcentral Gyrus	R	4.84	52	−30	60
Postcentral Gyrus	L	5.25	−60	−8	22
Supramarginal Gyrus and Parietal Operculum	L	5.62	−62	−30	28
Supramarginal Gyrus	L	7.75	−62	−32	44
Superior Parietal Lobule	R	8.59	14	−70	58
x Superior Parietal Cortex	R	5.79	18	−62	60
x Superior Parietal Cortex	R	5.08	18	−64	68
Right Superior Parietal Lobule	R	4.84	16	−54	70
Frontal Lobe					
Paracentral Lobule/Cingulate Cortex	R/M	7.49	6	−34	52
Cingulate Cortex	L/M	6.40	−6	−26	44
Inferior Frontal Gyrus–Pars Opercularis	R	6.06	56	12	12
Insular Lobe	L	5.60	−40	4	2
Temporal Lobe					
Superior Temporal Gyrus	R	5.48	44	−32	18
Occipital Lobe					
Middle Occipital Gyrus	L	5.31	−36	−86	36
Middle Occipital Gyrus	R	4.93	36	−80	46
Middle Occipital/Angular Gyrus	R	8.53	46	−80	28

Voxel threshold $P=0.05$ (FDR-corrected), cluster size threshold $k=10$. Anatomical location, stereotactic coordinates and t -values are provided for the peak voxel maxima in the respective cluster. L=left hemisphere, R=right hemisphere, M=medial activation, x=sub-peaks of a cluster.

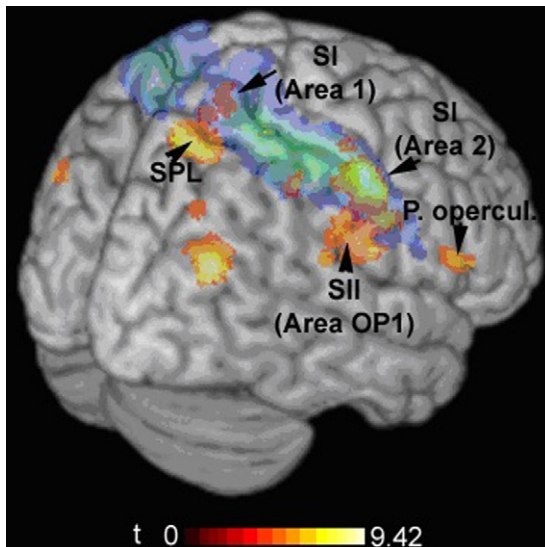


Fig. 5. Significantly stronger hemodynamic changes resulting from reaching range predictions than from the gender matching control condition (thresholded at $P=0.05$, FDR-corrected, $k=10$). Red to yellow colors indicate stronger signal in right superior parietal lobe, middle occipital gyrus, somatosensory cortex and pars opercularis/ventral premotor cortex. Blue to green colors delineate the somatosensory cortex (Area 2) as defined by probabilistic cytoarchitectonic mapping (Eickhoff et al., 2005). Area labels are derived from cytoarchitectonic mapping. SPL=Superior Parietal Lobe, P. opercul.=Pars opercularis, SI=primary somatosensory cortex, SII=secondary somatosensory cortex.

Contrasting the hand with the foot reaching condition revealed very few differences between the two conditions. Activation differences were largely confined to secondary visual areas of the occipital cortex, and the only significant difference in sensorimotor areas was obtained in the left parietal operculum (Area OP1) where the hemodynamic response was stronger in the foot reaching condition. Notably, this effect was due to a slight deactivation in this area in the hand reaching condition accompanied by a comparably low positive signal change for foot reaching. The latter was far below the signal changes observed in other brain regions when contrasting the experimental task with the fixation or the gender-matching controls. Note also that no activation differences whatsoever were found in primary motor or premotor areas. In addition, we performed detailed individual analyses of the contrasts reaching range (arm) > reaching range (leg) and vice versa for all 17 participants. None of these analyses showed a somatotopic pattern of activation, and most of the individual data showed no activation differences in primary sensorimotor areas at all.

3.2.3. Correlation with behavioral data and visual imagery scores

Correlating percentage correct with brain activity revealed significant positive correlations in medial primary and premotor areas (Area 4a, and SMA-proper), in bilateral secondary

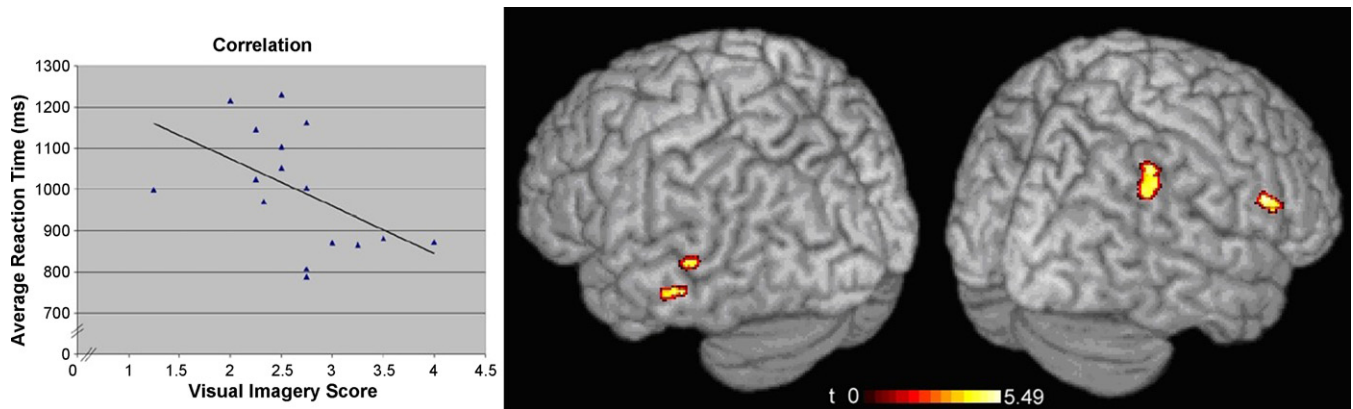


Fig. 6. Correlation between individual differences in visual imagery skill and speed of responses (left), and the corresponding significant correlation (right) of hemodynamic changes with visual imagery skill in left posterior temporal lobe (middle), right parietal lobe (parietal operculum) and right ventral premotor cortex (pars opercularis). Thresholded at $P=0.001$, uncorrected, $k=10$.

Table 2

Significant correlations ($P=0.001$, uncorrected, $k=10$) between hemodynamic responses (contrast reaching range/averaged > baseline) and the visual imagery subscale of Sheehan (1967)

Brain region	L/R	<i>t</i> -Value	MNI coordinates		
			<i>x</i>	<i>y</i>	<i>z</i>
Inferior Frontal/Pars Opercularis	R	5.49	54	4	22
Inferior Parietal Lobule	R	5.12	44	-50	44
x Angular Gyrus	R	4.75	35	-45	32
Middle Temporal Gyrus	L	4.77	-50	-34	-12
Middle/Superior Temporal Gyrus	L	4.56	-54	-42	6
Lingual Gyrus	R	4.72	10	-56	0

Stereotactic coordinates and *t*-values are provided for the local voxel maxima in the respective cluster. L = left hemisphere, R = right hemisphere, x = sub-peak of a cluster.

somatosensory cortex (Area OP1), in right primary somatosensory cortex (Area 3b; MNI coordinates *x/y/z*: 62/-10/30), in medial superior frontal gyrus (-4/40/30), as well as in perigenual and medial anterior cingulate cortex (-4/30/10; -6/2/34).

Significant positive correlations between hemodynamic responses and the visual imagery subscale of the Sheehan questionnaire were identified in right inferior parietal lobule/angular gyrus, right pars opercularis, left medial/superior temporal lobe, and in rostral lingual gyrus. About 77% of the activated voxels of the cluster in the parietal lobe were located within anterior intraparietal sulcus (human intraparietal area 2; Choi et al., 2006); the cluster in right ventral premotor cortex partially extended into Area 44, but was slightly more posterior and medial than the one detected by the contrast reaching range prediction/averaged > gender matching (see Figs. 5 and 6, Table 2).

4. Discussion

This study was designed to test two alternative hypotheses concerning the accomplishment of reaching range evaluations for others. One hypothesis claims that motor imagery plays a dominant role. This hypothesis predicts the involvement of medial and dorso-lateral premotor areas, the cerebellum, as well as of primary motor cortex, in a somatotopic manner. Stronger involvement of the mirror neuron system, the somatosensory cortex, and a lack of somatotopy is predicted by our alternative

hypothesis. This hypothesis combines the theory of common coding with the discovery of mirror neurons. It assumes that action understanding relies upon abstract coding of action goals and of action consequences, rendering a consideration of the specific kinematic properties of the involved movements unnecessary. Hence, one crucial difference between these two hypotheses is that one of them predicts activation in dorsal lateral and medial premotor areas, in the cerebellar cortex, and possibly also in primary motor cortex (in a somatotopic manner) – while the other hypothesis predicts stronger and non-somatopic activations in somatosensory areas and in the mirror neuron system (ventral premotor and inferior parietal cortex).

Where do the results of this first-ever functional neuroimaging study of reachability estimation leave these two competing hypotheses? A number of motor areas, including dorsal premotor cortex, which seems to be crucial in reaching movements, were activated when contrasting the experimental condition with the fixation baseline. This result would be in line with previous demonstrations that motor imagery is associated with increased hemodynamic activity in the cortical areas that are activated during actual execution of the imagined action (e.g., Ehrsson et al., 2003; Michelon et al., 2006; Porro, Cettolo, Francescano, & Baraldi, 2000; Roth et al., 1996; Ruby & Decety, 2001). However, when contrasting the experimental conditions with a condition controlling for various motor processes such as response preparation and the analysis of bodily features, no

significant signal changes remained in dorsal lateral, medial premotor, or primary motor cortices. Also, there was no evidence for cerebellar activation or a somatotopic activation in posterior parietal and frontal motor areas – even when analyzing the data on a single-subject level. The neuroimaging data therefore do not provide unanimous support for a motor imagery hypothesis in the sense that observers simulated the reaching movement from a first-person perspective.

Our data fit better with the common coding theory and the associated mirror-neuron system account of action understanding. Evidence for the latter is derived from the fact that reaching range predictions were specifically associated with activation in the right ventral premotor cortex and in bilateral supramarginal gyri. The ventral premotor activation is in line with a large number of neuroimaging studies documenting that the ventral premotor cortex is the human homologue of monkey F5 area, in which sensory-motor neurons code the goal of perceived and executed actions (Rizzolatti & Craighero, 2004). As shown by a meta-analysis, the pars opercularis in the inferior frontal gyrus of both hemispheres contributes to this aspect of the human mirror system during action observation and imitation (Molnar-Szakacs, Iacoboni, Koski, & Mazziotta, 2006). Moreover, a recent neuroimaging study indirectly indicates that activation in the right hemisphere is more pronounced and widespread when controlling for confounding effects of stimulus and response lateralities (Aziz-Zadeh, Koski, Zaidel, Mazziotta, & Iacoboni, 2006). The inferior parietal activations (supramarginal gyrus) observed in our study may also be ascribed to the mirror-neuron circuitry, as mirror neurons have been described in monkey's inferior parietal cortex (Fogassi et al., 2005). Notably, these neurons seem to play a particular role in the encoding of action goals. In addition, a recent fMRI study using the phenomenon of repetition suppression elegantly demonstrates that activation in left anterior and middle intraparietal sulcus is specifically related to the immediate goal of an observed grasping action—independently of the chosen movement trajectory (Hamilton & Grafton, 2006). Activations in our study are in line with this finding. Left-hemispheric parietal activations in our study were very close to the clusters detected by Hamilton and Grafton (2006) and encompassed them when the threshold was lowered, and activation clusters in right parietal cortex clearly included the anterior intraparietal sulcus.

Based upon previous imaging studies of motor imagery the lack of somatotopic activation may be surprising. Moreover, recent results showed somatotopically organized activation even when merely observing different body parts being touched or moved (Avikainen, Forss, & Hari, 2002; Blakemore, Bristow, Bird, Frith, & Ward, 2005; Möttönen, Järveläinen, Sams, & Hari, 2004). One might have expected somatotopic activation for reaching range *predictions* involving different limbs. However, no differences whatsoever were obtained in premotor or primary motor areas, not even on the single-subject level. This lack of somatotopic activation may provide further support for the common coding/mirror system account, which emphasizes the end over the means (i.e., the actual effectors used for the reaching movements). Still, it might be argued that a somatotopic activation pattern should be observed in somatosensory

cortex. Apart from the activation difference in SII, however, no such modulation of activation was observed. Nonetheless, several alternative explanations for the absence of *somatosensory* somatotopy should be considered. Touch in the current task might be represented on a more abstract level, and therefore does not necessarily involve the concrete effectors used in the two different conditions. This would be in line with the observation that secondary and not primary somatosensory cortex activation was modulated when contrasting the two conditions. In addition, the lack of somatotopic modulation might also be due to general interindividual variability in somatotopic maps. Indeed, one fMRI study investigated the response of the somatosensory cortex to different somatic stimuli applied to lips, face, trunk and foot (Disbrow, Roberts, & Krubitzer, 2000). One important finding of that study was that the pattern of activation generated by the same stimulus was highly variable across subjects. In addition, large overlaps between the representations of the different body parts in SII was found, which was interpreted to serve the purpose of integrating information across body parts. However, note that analyses of individual data did not yield any evidence for somatotopy, nor for any differences in activation in motor areas at all. Finally, both reaching tasks involve large parts of the human body and not only the hand or foot. Such movements would recruit large and adjacent portions of somatosensory cortex, blurring potential somatotopic organization patterns in the evaluation of these movements. Future studies may want to compare more confined reaching movements, as well as employ independent localizers of the sensorimotor representations involved in the to-be-evaluated reaching movements in order to take interindividual variability into account more explicitly.

Of special interest, the strongest signal increases related to reaching range predictions were detected in clusters located in left and right somatosensory cortex. We suggest that such activation reflects the abstract processing of the sensory consequences evoked by the potential action of others, as proposed by the common coding theory (Hommel et al., 2001; Hommel, 2004; Knoblich & Prinz, 2005; Prinz, 2003). Direct evidence for activation of somatosensory areas in the visual observation of touch has been provided in a number of fMRI studies (Blakemore et al., 2005; Keysers et al., 2004). However, in our study, the stimuli did not feature any perceivable contact between the models and the targets. We thus suggest that the involvement of the somatosensory cortex reflects anticipation of touch (i.e., the contact of hand or foot with the target; see also Field & Wann, 2005). Such a proposal is supported by studies demonstrating that SI and SII are activated by anticipation of touch in the absence of any tactile stimulation (e.g., Carlsson, Petrovic, Skare, Peterson, & Ingvar, 2000). Alternatively, somatosensory activation might be related to tactile imagery and attention to touch as these processes are known to trigger activation in primary and secondary somatosensory cortices (Johansen-Berg, Christensen, Woolrich, & Matthews, 2000; Oouchida et al., 2004; Yoo, Freeman, McCarthyIII, & Jolesz, 2003). Also, based on the effects of TMS on the visual enhancement of touch it has been suggested that SI might be part of a neural network encoding multisensory information related to the body

(Fiorio & Haggard, 2005). This might explain why somatosensory areas were also activated during the gender matching task.

It might be argued that the first-person simulation account also predicts somatosensory activation. On a theoretical level, activation of motor representations during motor imagery should also activate their associated somatosensory representations. However, empirical evidence concerning somatosensory activation during first-person motor imagery is inconsistent and seems to suggest that somatosensory areas are not reliably activated by motor imagery (e.g., Ehrsson et al., 2003; Michelon et al., 2006; but see also Ruby & Decety, 2001). In addition, a first-person simulation account would predict a somatotopic activation pattern in primary somatosensory areas on both a theoretical and an empirical level (e.g., Szameitat, Shen, & Sterr, 2007). We concede that the activation of somatosensory areas alone would not allow distinguishing between our two hypotheses—since depending on the theoretical stance adopted both might predict somatosensory activations (see also the recent discussion about the ability of brain imaging data to distinguish between psychological hypotheses, e.g., Coltheart, 2006). Even then, though, the clear absence of dorsal lateral premotor activation speaks against an explicit action simulation from a first-person perspective.

Finally, an apparent conflict between some of the behavioral data must be discussed. Suggestive of a motor imagery account, we found lower response latencies in the foot task, compared to the arm task. This result replicates findings of faster decisions for less complex motor imagery: rotations around the knee and ankle in the foot estimation task are easier to imagine than the more complex coordination of hip and shoulder rotations required for the hand estimation task (e.g., Johnson, 2000; Parsons, 2003). On the other hand the questionnaire data indicate that participants believed they used a visual imagery strategy. They reported to use visual imagery to ‘view’ the model reaching out to the target placed in front of it. These reports in turn match the correlation found between the participants’ visual imagery skills and the speed with which they solved a task, as participants with higher (self-reported) imagery skills were able to make faster reaching range predictions.

To decide between these two possibilities, it is informative to inspect the brain activation patterns. The large cluster in right superior parietal lobe (SPL) and the activation detected in the dorsal posterior cingulate cortex suggest a substantial role of brain areas involved in visuo-spatial information processing in solving the reachability estimation task. The role of the SPL in visuo-spatial information processing is well-documented. It is part of the so-called dorsal visual stream that is critically involved in perception-for-action representations—i.e., pragmatic representations that aid the transformation of visuo-spatial perceptions into actions in space (e.g., Milner & Goodale, 1998). The SPL also plays an important role in visual imagery, in particular when the task requires transformations of objects or body parts from an allocentric perspective (e.g., Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001; Parsons, 2003). It is worth noting that the current task required both estimating the spatial distance between model and target, as well as a pragmatic representation of the reaching action. Activations in

dorsal posterior cingulate cortex might serve a similar function, as this brain region has been assigned an important role in visuo-spatial orientation, and also has extensive connections with the parietal lobe (Vogt, 2005).

Interestingly, better visual imagery skills were also correlated with hemodynamic responses in the right inferior parietal cortex and in ventral premotor cortex, as well as in the medial-superior temporal gyrus. The adjacent superior temporal sulcus plays a special role in the visual analysis of actions (Puce & Perrett, 2003), coding the spatio-temporal interaction between the agent performing the action and the object of the action. Such coding may also be triggered by merely anticipating a potential action. Also, the cluster in the right inferior parietal region corresponds closely to the contralateral left-hemispheric activation encoding goals of right-handed actions detected by Hamilton and Grafton (2006). Thus, on the basis of combined behavioral and brain imaging data, it seems that visual instead of motor imagery contributes to efficient performance in reachability estimation for others. The difference in behavioral data may then be explained by the easier *visual* imagination and goal-directed encoding of the less complex foot movement.

Notably, this conclusion would again support the common coding notion that mirror neurons might provide a more or less automatic mapping from visual perception onto action simulation. Considering the available empirical and theoretical evidence, we therefore propose that reaching range evaluations are accomplished by a functional neural network involved in (a) action understanding (ventral premotor areas) and goal representation (intraparietal sulcus/supramarginal gyrus), in (b) processing visuo-spatial information and guiding perception for action (posterior cingulate and superior parietal lobe), and in (c) processing somatosensory representations associated with the anticipation and/or imagery of touch between the model’s effectors and the target objects. The relevance of the latter representations is also documented by the significant correlations between somatosensory signal changes and response accuracy. We speculate that predicting or not whether a touch between model and target would occur might be decisive for whether participants answer with yes or no. A more specific test of this hypothesis would, however, require a single-trial analysis of activation-response correlations. This analysis is precluded by the use of a block design which was optimized for detecting activation differences between the target conditions in the present study. Future studies should therefore address this issue by using an event-related design to assess parametric variation of activation with response accuracy. In addition, such a design would also allow to assess parametric variation of activation with target distance.

In conclusion, the fact that different brain systems are activated during reaching range predictions than during actual reaching movements speaks against a first-person motor imagery account. Rather, the pattern of brain activation we found is consistent with the common coding theory and the role of the mirror-neuron system and perception-action coupling in the prediction and understanding of the actions and intentions of others (e.g., Prinz, 2003; Rizzolatti & Craighero, 2004; Sommerville & Decety, 2006).

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