*Cerebral Cortex*, 2021;00: 1–14

https://doi.org/10.1093/cercor/bhab225
Original Article

ORIGINAL ARTICLE

# Action Observation Responses Are Influenced by Movement Kinematics and Target Identity

Helen E. Savaki[1,2,†], Eleftherios Kavroulakis[2,†], Efrosini Papadaki[2,3], Thomas G. Maris[2,3] and Panagiotis G. Simos[2,3]

[1]Institute of Applied and Computational Mathematics, Foundation for Research and Technology Hellas, Iraklion, Crete 70013, Greece, [2]Faculty of Medicine, School of Health Sciences, University of Crete, Iraklion, Crete 70013, Greece and [3]Computational Bio-Medicine Laboratory, Institute of Computer Science, Foundation for Research and Technology Hellas, Iraklion, Crete 70013, Greece

Address correspondence to Helen Savaki, Institute of Applied and Computational Mathematics, Foundation for Research and Technology Hellas, Iraklion, Crete 70013, Greece. Email: savaki@uoc.gr

[†]Helen E. Savaki and Eleftherios Kavroulakis have contributed equally to this work.

## Abstract

In order to inform the debate whether cortical areas related to action observation provide a pragmatic or a semantic representation of goal-directed actions, we performed 2 functional magnetic resonance imaging (fMRI) experiments in humans. The first experiment, involving observation of aimless arm movements, resulted in activation of most of the components known to support action execution and action observation. Given the absence of a target/goal in this experiment and the activation of parieto-premotor cortical areas, which were associated in the past with direction, amplitude, and velocity of movement of biological effectors, our findings suggest that during action observation we could be monitoring movement kinematics. With the second, double dissociation fMRI experiment, we revealed the components of the observation-related cortical network affected by 1) actions that have the same target/goal but different reaching and grasping kinematics and 2) actions that have very similar kinematics but different targets/goals. We found that certain areas related to action observation, including the mirror neuron ones, are informed about movement kinematics and/or target identity, hence providing a pragmatic rather than a semantic representation of goal-directed actions. Overall, our findings support a process-driven simulation-like mechanism of action understanding, in agreement with the theory of motor cognition, and question motor theories of action concept processing.

**Key words:** aimless motion, goal-directed actions, intransitive actions, movement kinematics, target identity

## Introduction

Action perception allows the observer to distinguish one action from another, to identify what and how it is done (e.g., grasping a cup to bring it to a target). Action understanding allows the observer to identify why an action is being done and involves detection of the actor's immediate goal and the actor's high-level intention. The "immediate goal" reflects a pragmatic representation of the action (e.g., bringing the cup to a person or to a bowl), whereas the "high-level intention" reflects a semantic representation of the act (e.g., drinking or pouring the liquid). While action semantics pertains to the representation of action concepts, thoughts, and intentions, action pragmatics refers to the representation of sensorimotor transformation, motor control, and movement execution (Prinz 2014). The aim of the present study was to investigate the mechanism that an observer is using to detect the actor's immediate goal: to explore which characteristics of the action are distinctly detected by the observer.

There are at least 2 different theories concerning action understanding. The first theory claims that mirror neurons in 2 specific areas of the brain (monkey brain areas F5 and PF/PFG) encode the actor's underlying motivation, and attribute intention to the actor, without the mediation of other cognitive processes (Rizzolatti and Sinigaglia 2007; Rizzolatti and Fogassi 2014). [Parenthetically, ventral premotor cortical area F5 and inferior parietal cortical area PF/PFG in monkeys correspond to human areas premotor BA6 (ventral premotor cortex [PMv]) and parietal BA40 (IPL) (Petrides and Pandya 1994; Tomaiuolo et al. 1999; Buccino et al. 2001; Petrides 2005)]. Therefore, according to this theory, mirror neuron areas encode semantic information of the observed action. Yet, it is not clear whether action "mirroring" in these 2 cortical areas reflects high-level intention understanding (Rizzolatti and Sinigaglia 2010) or simply low-level resonance mechanisms (Csibra 2007). Nor is it known whether mirror neurons encode a "vocabulary" of actions or goals/intentions (Fogassi et al. 2005; Bonini et al. 2010), "the subjective value" of observed actions paired with reward (Caggiano et al. 2012), or something "more idiosyncratic" to the particular action situation (Nelissen et al. 2005). However, it is known that the responses of mirror neurons depend on several factors beyond intention, such as handedness of the actor and direction of movement (Gallese et al. 1996), whether the action is executed in the peripersonal or extrapersonal space of the observer (Caggiano et al. 2009), and whether the action is presented from the first or third person perspective (Caggiano et al. 2011). Furthermore, it is known that inactivation of area F5, housing the mirror neurons, results in slowing down the movement and no other motor or cognitive deficit (Fogassi et al. 2001). Another problem is that "goals" and "intentions" have been used interchangeably in the mirror neuron literature, and the experiments concluding that mirror neurons encode "goals/intentions" have been heavily criticized due to lack of control of several variables. It has been argued that mirror responses in those experiments may reflect the identity of the object/target to be grasped (Ruggiero and Catmur 2018) and/or the kinematics of movement (Papadourakis and Raos 2017) rather than the intention of the actor proposed by Fogassi et al. (2005). Also, an early indication that mirror neurons did not respond to observation of intransitive actions was used to support the idea that mirror neurons represent intention and not kinematics (Gallese et al. 1996; Umilta et al. 2001; Rizzolatti and Sinigaglia 2016). However, it was recently demonstrated that mirror neurons respond to the observation of intransitive actions (Papadourakis and Raos 2017).

The second theory implies that pragmatic rather than semantic information is encoded in components of the action observation network, namely that contextual information (such as the employed object/target) and/or movement kinematics may contribute to action understanding. It was suggested that during action observation we may continually monitor the kinematic properties of movements in order to determine intention (McAleer et al. 2014). Indeed, actions performed with different intentions result in different kinematics, and consequently in perceptual differences (Georgiou et al. 2007; Becchio et al. 2008; Sartori et al. 2009; Naish et al. 2013), and activation of the observer's motor cortex is significantly correlated with the kinematics of the observed movement (Agosta et al. 2016). The reports above provide a kinematics-based view of action understanding. Moreover, it is known that object identity and grasp-relevant dimensions of objects to-be-grasped are encoded in the action observation system (Craighero et al. 2014; Monaco et al. 2014; Ruggiero and Catmur 2018), providing an object-based view of action understanding.

In an attempt to inform the current debate on the possible mechanisms underlying action understanding, we dissociated the 2 components of prehension, that is, the reaching (arm transport) from the grasping (hand grip) component. To this end, we first examined the effects of observing purposeless outreaching arm movements in the absence of any target (the so-called intransitive actions), to find out if any of the components of the observation network are activated by mere observation of aimless arm movements. In a separate session, we added 2 targets and a grasping component, to examine the effects of the target/goal and the kinematics during observation of goal-directed reach-to-grasp movements (the so-called transitive actions). In this study, when we use the term target/-goal, we refer to the final target of movement, which is also the immediate goal of action, and not to a high-order intention. The first functional magnetic resonance imaging (fMRI) experiment, involving observation of aimless arm movements in 2 consecutive reach directions, resulted in activation of most of the components reported to support action execution and action observation (Simos et al. 2017). Given the absence of a target/goal in this experiment, our finding is consistent with the view that during action observation we monitor movement kinematics. In the subsequent double dissociation fMRI experiment, we contrasted activation profiles as human participants observed goal-directed reach-to-grasp actions involving either different targets or different kinematics. The results revealed the components of the observation-related cortical network, which were affected by 1) actions that have the same target/goal but different reaching and grasping kinematics and 2) actions that have very similar kinematics but different targets/goals. Overall, our results demonstrate that action observation-related areas, including mirror neuron ones, are informed about movement kinematics and/or target identity, providing a pragmatic (sensorimotor) rather than a semantic (conceptual) representation of goal-directed actions.

## Materials and Methods

### Participants

Data were obtained from 21 volunteers recruited through advertisement in the Medical School (mean age = 28.4, standard deviation = 4.3 years; 11 men). Participants were screened for right handedness, negative history of neurological or psychiatric disorder, and regular use of any medication. They all had normal or corrected to normal vision and provided written consent in accordance to the Declaration of Helsinki. The study was approved by the ethics committees of 1) the University Hospital of Crete and 2) the Foundation for Research and Technology-Hellas.

### Tasks and Stimuli

In the first experiment, in order to examine the effects of observing non-goal-directed (intransitive) arm motion in the absence of any target/goal, the fMRI block design included four 35-s blocks of outreaching aimless arm movements alternating with four 35-s blocks of static baseline. The stimulus in "active" blocks consisted of 1) a disembodied arm/hand with extended wrist and fingers executing 2 successive reaching movements of different direction, from a resting position on a table, toward 2 different positions in space in the absence of any target, and 2) a fixed white cross at the center of the display (see video "aimless

**Table 1** Experimental conditions

| | Movement kinematics | | | Target/goal | |
|---|---|---|---|---|---|
| Condition | Reaching to cup | Grasping cup | Reaching to target/goal | Person | Bowl |
| Aimless motion | +* | - | +* | - | - |
| s-f P | Slow | Precision grip | Fast | + | - |
| f-s P | Fast | Whole hand | Slow | + | - |
| f-s B | Fast | Whole hand | Slow | - | + |

+* In the case of aimless motion, an arm/hand with extended fingers executes the same 2 reaching movements toward the position of the cup and the position of the final target/goal, in the absence of cup and final target/goal (see corresponding video in Supplementary Material). The s-f P and f-s P conditions have the same final target/goal (Person) but different kinematics (in both grasping and reaching components of movement), whereas the f-s P and f-s B conditions have the same kinematics (in both grasping and reaching) but different final target/goal (either a Person or a Bowl).

arm movements" in Supplementary Material). The duration of the first aimless reach movement was 1400 ms; average velocity = 0.36 m/s, whereas that of the second consecutive reach movement was 4033 ms in duration; average velocity = 0.12 m/s. The directions, speeds, and amplitudes of the 2 components of movement during these intransitive actions (in the absence of any target) approximated those during the 2 transitive conditions to specific targets (i: fast-slow to person, f-s P; and iii: fast to cup-slow to bowl, f-s B) as described below. Clip duration was 5433 ms, with a 400 ms blank screen between successive repetitions of each clip. The video clip was presented 6 times within each one of the 4 "active" blocks. The stimulus presented during the static "baseline" blocks of this task consisted of the first frame of the video clip, that is, a disembodied arm/hand with extended wrist and fingers resting on a table and a white cross at the center of the display (see video "aimless arm movements" in Supplementary Material). This stimulus was repeated 6 times (duration = 5433 ms) interspersed with a 400 ms blank screen.

In the second experiment, examining the effects of observing transitive goal-directed arm movements, the fMRI block design included 3 action observation tasks. Each task involved 4 "active" 35-s blocks alternating with four 35-s blocks of static baseline. During each "active" block, a video clip (a different one in each task) illustrating a 2-movement action sequence was presented 6 times. The 3 clips displayed 1) a disembodied hand relaxing at a table with a white tea cup next to it, 2) a fixed white cross at the center of the display presenting either the bust of a female person (in tasks i and ii) or a white ceramic bowl 30 cm in diameter (in task iii), and 3) either the bowl (in tasks i and ii) or the person (in task iii) right next to the central display. Arm movements toward both targets (cup and person/bowl) included transport components with different/controlled speeds (slow and fast) in 2 directions during the 2 successive movements. Also, grasps of the cup included 2 different/controlled grips (precision and whole hand grip). In other words,when the target was the same (person), in order to maximize the dissimilarity in kinematics between conditions s-f P and f-s P, not only the speed of reaching but also the type of grip differed by design. Table 1 demonstrates the variables of the different experimental tasks we used. Videos of all 3 conditions of the second experiment are provided in the Supplementary Material (see videos "fast-slow Person," "slow-fast Person," and "fast-slow Bowl" in Supplementary Material).

The observation tasks examining the effects of an action with the same goal (person) but different kinematics were the following: (i) fast to cup-slow to person and (ii) slow to cup-fast to person. It should be noted that task (iii) consisted of a rapid reaching movement toward the tea cup (1400 ms in duration; average velocity = 0.36 m/s), followed by grasping the cup with whole hand, and a much slower reaching movement bringing the cup over the edge of the bowl (4033 ms in duration; average velocity = 0.12 m/s). The bowl in condition (iii) was located in the center of the picture, that is, in the position of the person's head in conditions (i) and (ii), so that the kinematics of conditions (i) and (iii) were almost identical. This way, the target of the reaching movement was always at the center of the setting in all the tasks (i–iii). Clip duration was always 5433 ms, with a 400 ms blank screen between successive repetitions of each clip. Please note that 1) although both bowl and person were present in the picture, the visual environment was not exactly the same in tasks i and iii, because the target (person in task i and bowl in task iii) was always in the center of the frame, and 2) the direction, speed of movement, and grasping aperture were very similar, and not exactly the same, in the 2 tasks including different final targets. The stimulus in the static "baseline" blocks consisted of the first frame of the video clip from either conditions i–ii or condition iii, which was repeated 6 times (duration = 5433 ms) interspersed with a 400 ms blank screen. A sample sequence of frames is shown in Figure 1; and video clips of all experimental conditions are provided in Supplementary Material.

In all experiments, a white cross for fixation remained on the screen for the entire duration of the recording with the exception of a 3 s period between blocks during which a blank screen was presented to allow participants to move their eyes freely and blink if needed. Participants were asked to keep fixating the cross when appeared on the screen and keep their hands resting on their stomach. During the scan, stimuli were presented binocularly through a goggle system mounted on the head coil and controlled through the Nordic Activa (Nordic Neurolab, Bergen, Norway) software, which ensured precise timing of block onset/offset to the echo planar imaging (EPI) sequence.

Prior to the fMRI session, participants completed a 1-min practice run for each of the 4 tasks, outside the scanner, using the same device for stimulus presentation with that used during the EPI sequence, while EMG and eye movements were recorded. EMG was recorded from the extensor digitorum communis and the extensor indicis, through adhesive electrodes referenced to a third electrode placed on the lateral epicondyle. Muscle activity was not affected by any of the experiments in any of the subjects. Continuous EMG was recorded using a Nexus-4 device with a band pass setting between 20-200 Hz. Eye movements were

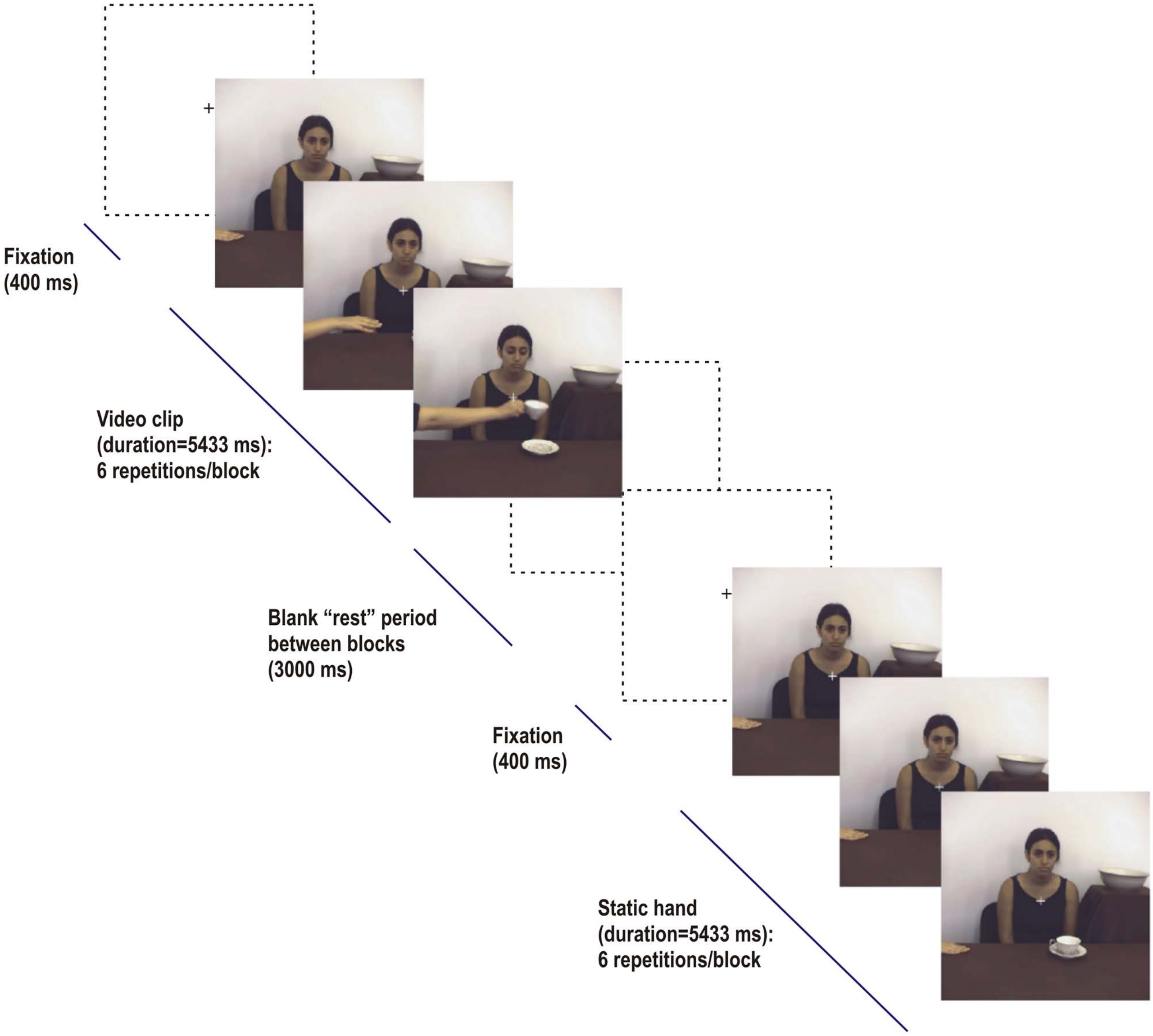

**Figure 1.** Sequence of frames during the s-f P task in the second experiment. To reduce complexity in the figure, the 400-ms fixation period between successive repetitions of the video clip (in active blocks) or the static hand frame (in reference/baseline blocks) was omitted.

recorded with an infrared camera mounted on the head coil to verify that all subjects could remain fixated on the target.

## Image Acquisition

Scanning was performed on an upgraded 1.5T Siemens Vision/-Sonata Hybrid clinical scanner (Erlangen, Germany) with powerful gradients (Gradient strength: 40 mT/m, Gradient rise time: 200 μs [fastest possible in 1.5T and 3T clinical systems], Gradient slew rate: 200 mT/m/ms) and a standard 4-channel head array coil. This upgrade (SIEMENS SONATA system gradients and SIEMENS EVOLVE packet) ensured improvement in temporal resolution (minimum TE 1.7 ms) by 30% and in spatial resolution by 20% (minimum voxel dimensions: 70 μm × 70 μm × 300 μm).

At first, a standard T2-weighted 2D-TSE-FLAIR (repetition time [TR]/echo time [TE]/inversion time [TI] = 9000/120/2600 ms) sequence with 4-mm transverse slices was performed, and the absence of any congenital anatomic variations or unexpected pathology was confirmed. For the blood oxygen level-dependent (BOLD)-fMRI, a T2*-weighted, fat-saturated 2D-FID-EPI sequence was used with the following parameters: TR 3500 ms, TE 50 ms, field of view (FOV) 192 × 192 × 108 (*x*, *y*, *z*), and acquisition voxel size 3 × 3 × 3 mm. Whole-brain scans consisted of 36 transverse slices with 3.0-mm slice thickness and no interslice gap. Each BOLD time series was 4.67 min in duration and consisted of 80 dynamic volumes (plus 4 dummy volumes to allow the signal to reach steady state). Additionally, high-resolution anatomical images were acquired sagittally, using a 3D magnetization-prepared rapid acquisition gradient echo sequence with the following parameters: TR 9.8 ms, TE 4.6 ms, flip angle 8°, TI 922 ms, FOV 180 × 230 (*x*, *z*), with acquisition voxel size of 0.98 × 0.98 (*x*, *z*) and slice thickness of 1 mm. The FOV covered the entire brain with the exception of the caudal-most aspect of the cerebellum (lobule VIII).

### Preprocessing and Analyses

Image processing and statistical analyses were performed in SPM12 (Statistical Parametric Mapping software, SPM: Welcome Department of Imaging Neuroscience, London, UK; available at: http://www.fil.ion.ucl.ac.uk/spm/). Initially, EPI scans were spatially realigned to the first image of the first time series using second degree B-spline interpolation algorithms and motion corrected through rigid body transformations (3 translations and 3 rotations about each axis). Next, images were spatially normalized to a common brain space (Montreal Neurological Institute template) and smoothed using an isotropic Gaussian filter (full-width at half-maximum = 7 mm). The BOLD signal was high pass filtered to remove low-frequency drifts with a time constant of 128 s.

For each task and participant, a fixed-effects general linear model (GLM; Friston et al. 1995) was fit to the data in SPM12, which allows the BOLD signal associated with each "active" block and with the preceding static baseline blocks to be convolved with the SPM12 standard hemodynamic response function. The model included 2 condition regressors of interest (active, static) and 6 motion regressors of no interest. Contrasts of interest (f-s P, s-f P, f-s B, and aimless movement) versus the corresponding static baseline were thresholded at $P < 0.05$ corrected for multiple comparisons. The reverse contrasts were also computed to ensure the appropriateness of the static baseline condition ("active" blocks < static baseline). Individual contrast *t*-value images were input to the second-level random effect analysis to estimate the generalizability of activations. Second-level activations were assessed for statistical significance applying a threshold of $P < 0.05$ with family-wise error (FWE) correction for multiple comparisons at the cluster level with an initial voxel-wise threshold of $P = 0.001$. Monte Carlo simulation (Slotnick et al. 2003; Slotnick 2017) was applied when necessary (in cases where voxel clusters were smaller than the minimum number required to obtain FWE-adjusted significance of $P < 0.05$) using the estimated smoothness of our functional data (10 mm). This resulted in a minimal cluster size of 58 voxels at a threshold of $P < 0.001$ uncorrected to achieve correction for multiple comparisons for $P < 0.05$. Anatomic identification of active clusters was performed using the SPM Anatomy Toolbox (Eickhoff et al. 2005).

Given that clusters of activated voxels in the first-level analyses in some areas of interest (especially in PMv, IPLv, TPj, SI) were small in extent and displayed considerable anatomic variability across participants, we did not perform second-level pairwise task comparisons using whole-brain contrast maps. Instead, we created individualized overlay masks of active voxels at a more liberal threshold ($P < 0.01$) for 2 pairs of first-level contrast maps (f-s P vs. s-f P and f-s P vs. f-s B). These masks were restricted to regions displaying significant activation in whole-brain one-sample *t*-tests (as described in the previous paragraph with certain exceptions presented in Results). For each individually drawn ROI, first-level contrast values were extracted and submitted to paired-sample *t*-tests evaluated at Bonferroni-adjusted 0.0036 (for 14 multiple comparisons).

In supplementary analyses, we estimated signal power in the frequency range covering the first harmonic of video clip presentation rate within "active" blocks (0.086 Hz) in 2 partially overlapping frequency bands (0.07–0.11 Hz and 0.09–0.13 Hz). Power estimates were computed for single-voxel band-passed time series (using a fourth-order Butterworth filter) in these nominal frequency ranges and then averaged over voxels within the individually drawn ROI masks as described in the previous paragraph. Pairwise statistical comparisons (f-s P vs. s-f P and f-s P vs. f-s B) were restricted to ROIs in anatomical regions where significant group-level activations were noted in whole-brain one-sample *t*-tests (listed in Tables 2 and 3).

## Results

### Observation of Intransitive Actions (Aimless Arm Movements)

As indicated by significant GLM effects ($P < 0.05$ FWE corrected), the observation of aimless arm/hand movements in the absence of any target was associated with increased BOLD signal, as compared to the corresponding static baseline, in several brain areas, which were previously found to support execution and observation of goal-directed actions (Simos et al. 2017). These brain areas included: the extrastriate body area/middle temporal cortex (EBA/MT; BA37), the inferior temporal gyrus/fusiform gyrus (ITG/FG; BA37), the superior parietal lobule (SPL; BA7), the dorsal and ventral inferior parietal lobule (IPLd, IPLv; BA 40), and the dorsal premotor cortex (PMd; BA6) bilaterally, as well as the primary somatosensory cortex (SI; BA3) in the left hemisphere and the temporoparietal junction (TPj; BA22) in the right hemisphere (see Table 2 and Fig. 2). The PMv (BA6) was activated only at the uncorrected level ($P < 0.001$, cluster size 23 voxels). The coordinates of the cluster center in BA37 (EBA/MT) in our study are within the probabilistic limits of area MT derived from myeloarchitectonic data (Malikovic et al. 2007; Bridge et al. 2014) and closely match the coordinates summarized for EBA (Ferri et al. 2013; Simos et al. 2017). Given the significant overlap between voxels activated by body parts and motion (Spiridon et al. 2006; Ferri et al. 2013), we henceforth refer to the latter activation in our study as EBA/MT. Also, the coordinates of the activated cluster center in BA22 (TPj) in our study match those reported earlier for TPj (Arzy et al. 2006; Blanke et al. 2010; Simos et al. 2017). The coordinates of cluster center located in SI closely match those reported for hand movement in previous studies (Lotze et al. 2000; Indovina and Sanes 2001; Simos et al. 2017). Finally, the coordinates of activated cluster in the lateral PM (PMd, PMv) are according to the distributional boundaries estimated earlier (Mayka et al. 2006; Simos et al. 2017).

### Observation of Transitive Actions (Goal-Directed Reach-to-Grasp Movements)

As indicated by significant GLM effects ($P < 0.05$ corrected), and shown in Table 3 and Figure 3, each 1 of the 3 tasks of observation of transitive actions (f-s P, s-f P, f-s B), when compared to the static baseline, resulted in clusters of significantly activated voxels in several cortical regions across the brain. In effect, all areas activated in the present study were previously demonstrated to support execution and observation of goal-directed actions (Simos et al. 2017). Interestingly, all areas activated by the observation of transitive actions (Table 3) were also activated for observation of intransitive movements in our study (Table 2), with the exception of PMv and certain higher order prefrontal association areas, which were affected only by observation of goal-directed actions and not by observation of mere arm transport.

### Kinematics-Related Contrasts (Different Kinematics but Same Target/Goal)

*GLM Model*

Whole-brain second-level analyses ($P < 0.05$ corrected) served to identify anatomic regions that displayed significantly active

**Table 2** MNI coordinates and *T* values of significant activations in whole-brain during observation of aimless arm movements; second-level analyses

| | | | Aimless motion | | | |
|---|---|---|---|---|---|---|
| Brain area | BA | Hem | x | y | z | T |
| EBA/MT | 37 | L | −50 | −72 | 0 | 10.06 |
| EBA/MT | 37 | R | 52 | −62 | 0 | 11.80 |
| ITG/FG | 37 | L | −48 | −58 | −20 | 4.32 |
| ITG/FG | 37 | R | 42 | −60 | −20 | 4.74 |
| TPj | 22 | R | 58 | −37 | 20 | 5.50 |
| SPL | 7 | L | −28 | −50 | 50 | 7.69 |
| SPL | 7 | R | 18 | −56 | 66 | 9.70 |
| IPLd | 40 | L | −30 | −52 | 54 | 8.04 |
| IPLd | 40 | R | 34 | −46 | 54 | 6.73 |
| IPLv | 40 | L | −54 | −28 | 38 | 4.75 |
| IPLv | 40 | R | 48 | −46 | 32 | 4.26 |
| SI | 3 | L | −50 | −25 | 38 | 4.97 |
| PMd | 6 | L | −30 | −10 | 48 | 6.56 |
| PMd | 6 | R | 36 | −6 | 52 | 5.16 |
| V3 | 19 | R | 36 | −80 | −2 | 4.18 |
| V3 | 19 | L | −36 | −80 | −2 | 4.93 |
| V1 | 17 | L | −12 | −98 | −6 | 4.84 |
| V2 | 18 | R | 22 | −74 | −6 | 5.68 |

*Note*: All activations shown here were corrected for multiple comparisons at the FWE $P < 0.05$. BA, Brodmann area; Hem, hemisphere; L, left; R, right.

**Table 3** MNI coordinates and *T* values of significant activations during observation of 3 types of goal-directed actions, in whole-brain; second-level analyses

| | | | s-f P | | | | f-s P | | | | f-s B | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Brain area | BA | Hem | x | y | z | T | x | y | z | T | x | y | z | T |
| EBA/MT | 37 | L | −50 | −72 | 6 | 10.98 | −50 | −72 | 4 | 9.14 | −52 | −72 | 6 | 12.03 |
| EBA/MT | 37 | R | 46 | −64 | 8 | 11.72 | 50 | −66 | 4 | 14.66 | 46 | −60 | 10 | 12.78 |
| ITG/FG | 37 | L | −42 | −80 | −6 | 7.30 | −50 | −70 | −12 | 6.51 | −48 | −70 | −12 | 6.66 |
| ITG/FG | 37 | R | 50 | −70 | −6 | 7.70 | 50 | −68 | −12 | 7.62 | 46 | −66 | −12 | 6.67 |
| TPj | 22 | R | 61 | −38 | 18 | 8.22 | 60 | −38 | 18 | 6.86 | 58 | −42 | 14 | 5.10 |
| SPL | 7 | L | −18 | −64 | 56 | 4.86 | −32 | −50 | 56 | 6.67 | −24 | −52 | 52 | 9.67 |
| SPL | 7 | R | 28 | −58 | 60 | 6.29 | 22 | −54 | 60 | 7.24 | 20 | −58 | 60 | 9.99 |
| IPLd | 40 | L | −26 | −40 | 54 | 6.33 | −32 | −48 | 56 | 7.24 | −24 | −52 | 54 | 10.10 |
| IPLd | 40 | R | 32 | −40 | 56 | 7.12 | 34 | −50 | 58 | 6.49 | 34 | −50 | 60 | 7.69 |
| IPLv | 40 | L | −56 | −38 | 34 | 5.06 | −54 | −30 | 34 | 6.41 | −52 | −36 | 40 | 5.59 |
| SI | 3 | L | — | — | — | — | −48 | −26 | 36 | 7.66 | — | — | — | — |
| PMd | 6 | L | −26 | −6 | 64 | 4.31[a] | −34 | −8 | 52 | 6.82 | −26 | −10 | 50 | 6.03 |
| PMd | 6 | R | 40 | −4 | 58 | 6.58 | 36 | −4 | 48 | 6.72 | 42 | 0 | 56 | 5.63 |
| PMv | 6 | L | — | — | — | — | −60 | 6 | 28 | 6.35[a] | −42 | 4 | 32 | 4.44[a] |
| PMv | 6 | R | 42 | 8 | 24 | 5.15[a] | — | — | — | — | — | — | — | — |
| SMA | 6 | L | 0 | −2 | 68 | 4.67 | — | — | — | — | — | — | — | — |
| SMA | 6 | R | 14 | 2 | 60 | 6.02 | — | — | — | — | — | — | — | — |
| IFG | 45 | R | — | — | — | — | — | — | — | — | 48 | 48 | −2 | 4.31 |
| MFG | 9/10 | L | — | — | — | — | — | — | — | — | −42 | 48 | −2 | 6.96 |
| MFG | 9/10 | R | — | — | — | — | — | — | — | — | 38 | 58 | −2 | 4.36 |
| SFG | 10 | R | — | — | — | — | — | — | — | — | 36 | 58 | 12 | 4.62 |
| MFG | 8 | L | — | — | — | — | — | — | — | — | −42 | 12 | 42 | 4.33[a] |
| MFG | 8 | R | — | — | — | — | — | — | — | — | 50 | 16 | 42 | 6.08 |
| V3 | 19 | L | −44 | −80 | −4 | 6.29 | −38 | −80 | −2 | 6.26 | −38 | −78 | −4 | 3.71 |
| V3 | 19 | R | 44 | −80 | −4 | 3.94 | 38 | −80 | −2 | 3.88 | 40 | −76 | −4 | 3.75 |
| V2 | 18 | R | 22 | −76 | −6 | 3.98 | 22 | −76 | −6 | 4.01 | 22 | −76 | −6 | 3.74 |
| V1 | 17 | L | — | — | — | — | −12 | −98 | −6 | 3.86 | −12 | −96 | −6 | 3.72 |
| V1 | 17 | R | 6 | −92 | 6 | 7.68 | 14 | −88 | −6 | 3.7 | 16 | −88 | −6 | 3.86 |

*Note*: Activations shown here were corrected for multiple comparisons at the FWE $P < 0.05$. SFG, superior frontal gyrus; SMA, supplementary motor area. Rest of abbreviations as in the footnote of Table 2. [a] Significant activation after Monte Carlo simulation (threshold 58 voxels).

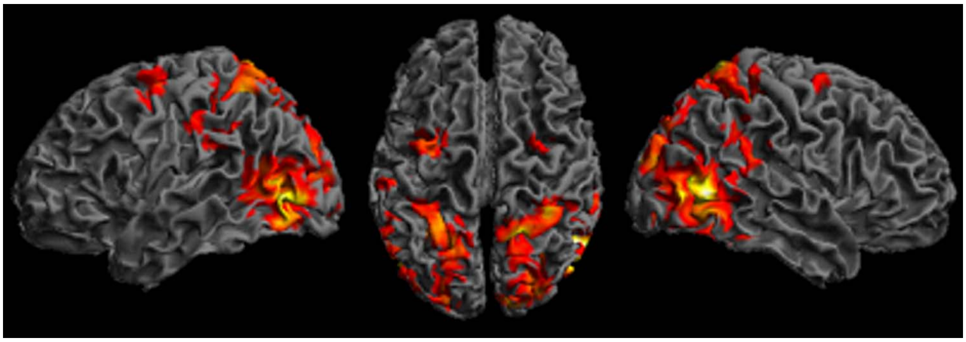

**Figure 2.** 3D rendering of significantly activated voxel clusters during observation of aimless arm movements as compared to the static control baseline, via whole-brain analyses. Lateral view of the left and right hemispheres and top view of the brain ($P < 0.05$ corrected).

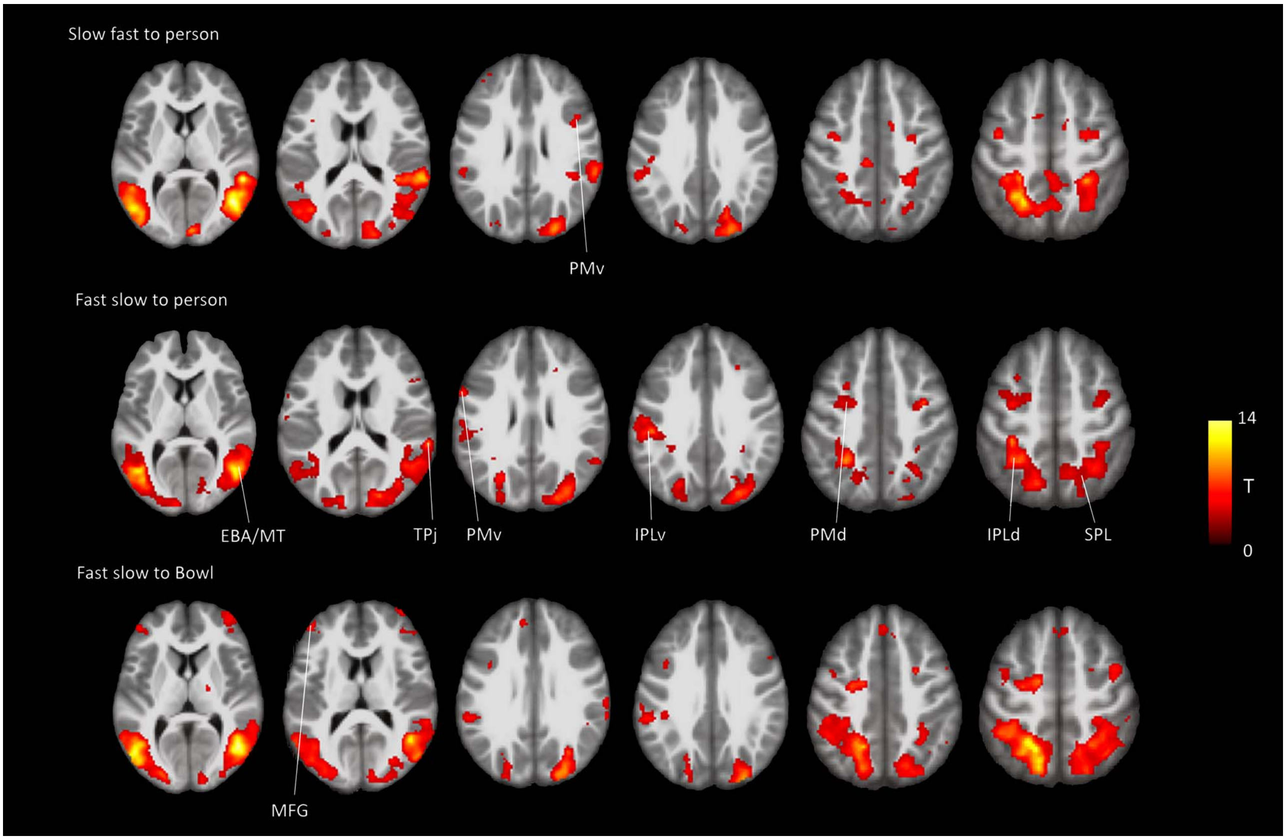

**Figure 3.** Clusters of significantly activated voxels during observation of 3 types of goal-directed actions as compared with the corresponding static baseline, via whole-brain analyses: (i) s-f P, (ii) f-s P, and (iii) f-s B action ($P < 0.05$ corrected).

voxel clusters, as compared with the static baseline, in response to the observation of each 1 of the 2 person-directed actions: slow-fast to person (s-f P) and f-s P. Significant clusters of active voxels were found in EBA, ITG/FG, SPL, IPLd, and PMd, bilaterally as well as in the right TPj, left IPLv in both person-directed conditions, and in the left SI in the f-s P condition. The right PMv was activated in s-f P condition and the left PMv in the f-s P condition (Table 3; Fig. 3). Moreover, observation of person-directed actions induced significantly active voxel clusters in the supplementary motor area (BA 6) bilaterally in the f-s P condition (Table 3).

*ROI Analyses*

In order to ensure that pairwise comparisons on the degree of signal increase between conditions actually reflected hemodynamic activity within the same cortical patch (in anatomical regions identified through GLM analyses), we performed pair-wise *t*-tests on voxel-level data derived at the subject level. Activity clusters were considered in 5 regions bilaterally (EBA/MT, SPL, IPLd, PMd, PMv), as well as in the left IPLv, left SI, and right TPj.

For comparison purposes (although second-level analyses failed to reveal significant activation), we also measured contrast values in subthreshold clusters in the right IPLv ($P < 0.01$, uncorrected in first-level one-sample $t$-tests). Visual inspection of activity clusters using a more liberal threshold at $P < 0.01$ confirmed varying degrees of spatial overlap between the 2 conditions in each 1 of the 14 regions shown in the upper panel of Figure 4. Next, we constructed subject- and region-specific anatomic masks each defined by the area of active-voxel overlap between the 2 conditions and computed the average contrast value across all voxels comprising the intersection of the 2 activity clusters within each region. Finally, we computed paired-sample $t$-tests to compare the degree of signal increase between the 2 conditions (evaluated at Bonferroni-adjusted $P < 0.0036$). Results revealed that the s-f P condition elicited increased signal as compared with the f-s P condition in the EBA, TPj, PMd, and PMv, all in the right hemisphere (Fig. 4 upper panel).

### *Low-Frequency Signal Amplitude Modulation Analyses*

In supplementary analyses, we compared the 2 conditions on the average power of low-frequency fluctuations computed across voxels within each set of region-specific overlap cluster (as defined above). Significantly elevated signal amplitude variability between 0.07 and 0.13 Hz was noted in the s-f P as compared with f-s P in the right PMv and PMd and bilaterally in IPLd and EBA (at $P < 0.0036$).

## Goal-Related Contrasts (Different Target/Goal but Very Similar Kinematics)

### *GLM Analyses*

Whole-brain second-level analyses ($P < 0.05$ corrected) served to identify anatomic regions that displayed significantly active voxel clusters, as compared with the static baseline, in response to the observation of each 1 of 2 actions that differed in goal and were matched for kinematics: f-s P and f-s B. Clusters of significantly active voxels, in both goal-directed conditions, were found in the EBA, ITG/FG, SPL, IPLd, and PMd, bilaterally, as well as in the right TPj, left IPLv, and left PMv. Significant activation within the left SI was found only in the f-s P condition (Table 3; Fig. 3). Moreover, clusters of significantly active voxels were found in the right inferior frontal gyrus (IFG; BA 45), the right superior frontal gyrus (BA 10), and bilaterally in middle frontal gyrus (MFG; BA8, and BA9/10) only in the f-s B condition.

### *ROI Analyses*

Using the procedure outlined above (in section Kinematics-Related Contrasts), we compared the 2 goal-directed conditions on the degree of signal increase derived from subject-specific overlay masks. Activity clusters were considered in 4 regions bilaterally (EBA/MT, SPL, IPLd, PMd), as well as in the right TPj, and left SI, left PMv, and left IPLv. For comparison purposes (although second-level analyses failed to reveal significant activation), we also measured contrast values in subthreshold clusters in the right IPLv and right PMv ($P < 0.01$, uncorrected in first-level one-sample $t$-tests). Results revealed that the f-s B condition elicited increased signal as compared with the f-s P condition in 2 right hemisphere areas (TPj, IPLv) and in 2 left hemisphere areas (IPLd, PMd). We also found that the degree of signal increase within commonly active voxels in the left SI was higher in f-s P than in f-s B (Fig. 4 lower panel).

### *Low-Frequency Signal Amplitude Modulation Analyses*

Supplementary analyses provided corroborating evidence of significantly higher low-frequency fluctuations between 0.07 and 0.13 Hz in the f-s B condition as compared with the f-s P condition in EBA, IPLd, and PMd, bilaterally. However, there was also evidence of increased signal amplitude variability in the same direction in the left PMv (where only a trend was noted in the analyses on first-level contrast values; see Fig. 4 lower panel).

## Discussion

In the present study, we examined whether the human brain areas engaged in action observation are affected by the kinematics and/or the identity of the target/goal of the observed action.

The first fMRI experiment, examining the effects of movement kinematics during action observation, involved observation of aimless arm movements in the absence of any target/-goal.

The second, double dissociation fMRI experiment, involved 2 types of goal-directed actions, namely 1) actions with 2 different targets/goals (Person or Bowl) while the action kinematics were very similar and 2) actions with 2 different movement kinematics (in both reaching and grasping components) while the target/goal was the same (Person). This way we identified the components of the observation-related cortical network, which were affected by 1) the identity of the target and/or 2) the kinematics of the observed action.

## Observation of Intransitive Actions (Aimless Arm Movements)

Observation of aimless reaching-out arm movements in the absence of any target/goal (Table 2) elicited fronto-parieto-temporal cortical activations, similar to those induced by observation of goal-directed reaching-to-grasp movements (Table 3). Our results are compatible with a monkey study, reporting that mere observation of an arm executing goalless movements recruited a cortical network overlapping extensively with that supporting execution and observation of goal-directed forelimb actions (Raos et al. 2014). Interestingly, in both monkey and human studies, this overlap did not include the association prefrontal areas, known to be involved in on-line monitoring and manipulating visual information related to goal-directed actions (Petrides 1994b, 1994a). More specifically, our finding that MT/EBA is activated during observation of aimless arm-motion complements studies reporting its involvement in visual processing of human body parts (Peelen and Downing 2007; Weiner and Grill-Spector 2013). Activation of the right-TPj is compatible with its association with the perception of biological motion in monkeys (Perrett et al. 1989) and in humans (Vaina et al. 2001). Activation of the PM is in agreement with its causal relation to deficits in perception of biological motion (Sakreida et al. 2005; Saygin 2007) and may reflect selectivity for hand kinematics as demonstrated for the monkey primary motor cortex (Georgopoulos et al. 1986; Georgopoulos 1991, 2003). Activation of IPL and SPL is compatible with the reports that 1) monkey parietal areas AIP and PFG (reciprocally connected with F5; Petrides and Pandya 1984) respond to visual presentation of intransitive hand actions (Maeda et al. 2015), 2) viewing body parts in motion induces activation of parietal areas in humans (Engel et al. 2008; Casile et al. 2010), and 3) movement direction is processed in the parietal cortex (Fabbri et al. 2010;

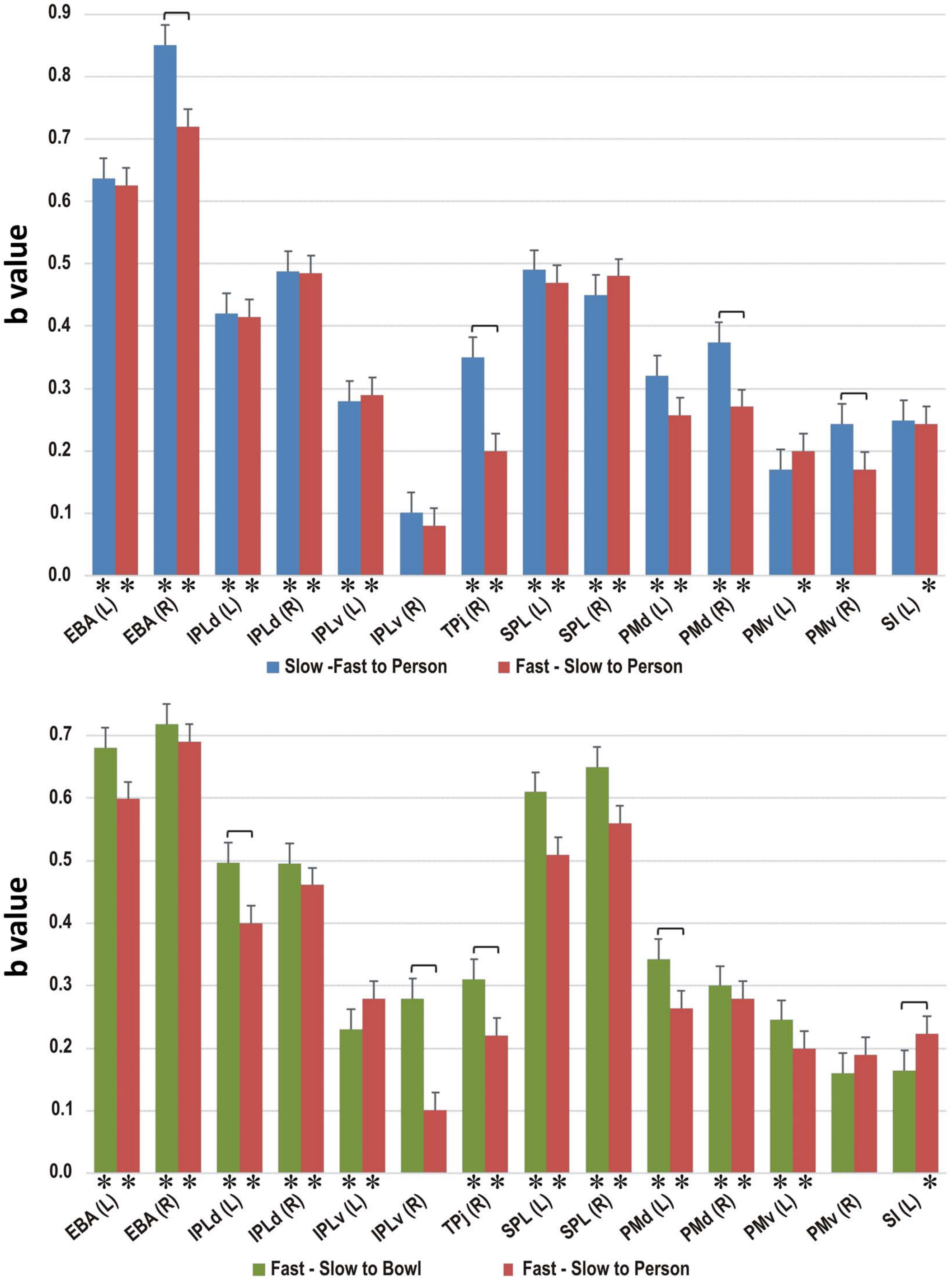

**Figure 4.** ROI analyses. Group-average first-level contrast values, compared with the static baseline in each condition, for voxels included in the intersection of significantly active clusters (identified at $P < 0.01$ uncorrected in one-sample *t*-tests at first-level analyses). Upper panel: Voxels in the 2 conditions involving person-directed movements (varying in kinematics); lower panel: voxels in the 2 conditions involving goal-directed movements (varying in target/goal and matched for kinematics). Brackets indicate pairs of contrast values that are significantly different from each other (Bonferroni-corrected $P < 0.0036$). Asterisks indicate regions where whole-brain GLM analyses revealed significant activation (compared with the static baseline at $P < 0.05$ corrected).

Davare et al. 2015) with kinematics used to read intention of the observed act (Koul et al. 2018). Actually, activation of SPL and PMd agrees with the notion that these areas encode movement velocity of the biological effector during observation of reaching (Di Dio et al. 2013). On the other hand, the activation of IPL and PMv in monkeys (Raos et al. 2014) as well as in humans (although only at the uncorrected level for PMv) during observation of aimless movements in the absence of any target contradicts the prevalent claim that a prerequisite of triggering mirror-neuron areas is the preshaping of the hand and its interaction with the object/target (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996; Rizzolatti and Fogassi 2014). Finally, activation of SI is compatible with the report that this area is engaged in observation of proximal compared to distal motion (Sakreida et al. 2005).

In summary, we demonstrated that 1) observation of aimless outreaching arm movements, in the absence of any target/-goal, elicits fronto-parieto-temporal cortical activations similar to those induced by observation of goal-directed reaching-to-grasp movements and 2) preshaping of the hand and hand interaction with the object/target are not prerequisites of triggering areas with mirror neurons.

## Observation of Transitive Actions (Goal-Directed Arm Movements)

Our results concerning cortical activations induced by observation of goal-directed arm movements are compatible with previous fragmentary reports (see reviews Grezes and Decety 2001; Caspers et al. 2010; Molenberghs et al. 2012; Hardwick et al. 2018; Koul et al. 2018). The present results agree well with those in our previous studies in humans (Simos et al. 2017) and nonhuman primates (for reviews see Savaki 2010; Savaki and Raos 2019). Moreover, activation of SI, SPL, and IPL agrees with the fact that parietal lesions alter the representational aspects of gestures (Sirigu et al. 1995, 1996, 1999). Activation of SI agrees with the reported effector-related somatosensory properties during action observation (Keysers et al. 2004) and may reflect descending, from higher cortical levels, somatosensory predictions. Activation of SPL may reflect the combination of past and present sensory information for decision-making, as demonstrated in monkeys (Romo et al. 2002, 2012; Romo and de Lafuente 2013), and/or the interaction between target location and movement direction, as demonstrated in humans (Barany et al. 2014). Activation of the EBA/MT agrees with previous reports concerning its selective response to observation of human limb movements (Filimon et al. 2007; Gazzola and Keysers 2009). Activation of the right-TPj is consistent with reports associating it to body knowledge, self-awareness, and perspective taking (Decety and Sommerville 2003; Van Overwalle and Baetens 2009; Sowden and Catmur 2015). Furthermore, the involvement of both PMd and PMv in transitive actions in our study is in agreement with previous studies reporting evidence against the existence of dedicated circuits for reaching and grasping (Cavina-Pratesi et al. 2010; Monaco et al. 2011; Fabbri et al. 2014). Remarkably, prefrontal cortices such as MFG and IFG were activated only for goal-directed actions. These findings support the suggestions that MFG contains action-related information held in working memory (Petrides 1996, 2005) useful for action understanding and that both IFG and MFG contain intention-specifying information (Becchio et al. 2012) conveyed by visual kinematics (Koul et al. 2018). We cannot rule out the possibility that the effect on BA8 reflects the contribution of gaze shifts. Also we cannot exclude the possibility that part of the activation of the arcuate sulcus is due to shifts of the line of sight (Amiez and Petrides 2009). However, the fact that the same premotor areas were activated by aimless motion, when the subject was looking straight ahead without any shift of gaze, indicates that the arcuate effects are mostly associated with the arm movements rather than gaze shifts. Finally, our results are in general agreement with a previous study on the neural substrate of gesture recognition, which reports a common network underlying the recognition of transitive, intransitive, and meaningless gestures independent of their type (Villarreal et al. 2008).

In summary, observation of transitive actions elicited cortical activations 1) similar to those induced by intransitive movements, with the exception of prefrontal areas, and 2) similar to those induced by action execution.

## Different Kinematics but Same Target/Goal

Kinematics-related activation of PMd, PMv, TPj, and EBA during the observation of goal-directed actions is supported by 2 lines of evidence: 1) contrast values and 2) low-frequency signal amplitude modulation. Modulation of the PMd-activation by movement kinematics in the observers' brain, when the goal of movement remained the same, is compatible with the report that the kinematic laws of human movements modulate responses in PMd during action observation (Casile et al. 2010) and that activity in PMd is modified by the amplitude of observed kinematic errors (Malfait et al. 2009). Our finding that PMv detects dissimilarities in movement kinematics is compatible with a recent single-cell recording study in nonhuman primates, which demonstrated that mirror neurons in area F5 (corresponding to the human PMv; Tomaiuolo et al. 1999; Petrides 2005) provide a kinematics-based representation of actions (Papadourakis and Raos 2017). The prominent activation of the EBA is in accordance with reports about its contributions to action attribution to the correct agent (Jeannerod 2004; Myers and Sowden 2008; Savaki and Raos 2019). Here, we demonstrated for the first time that EBA is informed about dissimilarities in movement kinematics of the actor during action observation and therefore may contribute to action understanding. Similarly, the finding that the right-TPj is informed about dissimilarities in movement kinematics complements the report that this area contributes to discrimination of the actor's intention (Becchio et al. 2012). Overall, our finding that movement kinematics modify several activations induced by observation of goal-directed actions complements several previous reports. For example, observers can use actor's kinematics to discriminate the intention of the action in the absence of contextual information (Cavallo et al. 2016), to predict the weight of the object an actor is lifting (Hamilton et al. 2007), and whether the actor is reaching for a large or a small invisible object (Ansuini et al. 2016). Observers can use action kinematics to distinguish between cooperative and competing movements (Manera et al. 2011; Sartori et al. 2011), to judge the quality of professional poker players (Slepian et al. 2013), and to predict the accuracy of a free throw (Aglioti et al. 2008). Also, movement kinematics is influenced by the social context (Krishnan-Barman et al. 2017) and the intention of action (Marteniuk et al. 1987), whereas our ability to perceive others' intentions is related to our competence to detect dissimilarities of kinematics (Ansuini et al. 2014).

In summary, areas engaged in action observation are informed about kinematic dissimilarities, and this information may be used to shape action recognition. This finding provides considerable support to the proposed process-driven simulation-like mechanism of action understanding (Savaki 2010; Savaki and Raos 2019).

## Different Target/Goal but Very Similar Kinematics

Both contrast values and low-frequency signal amplitude modulation revealed that during observation of goal-directed action, the activation of areas IPLd, IPLv, TPj, PMd, and SI was modulated significantly when we modified the target/goal of the movement while movement kinematics was very similar. Our finding that areas SI and PMd detect dissimilarities in targets/goals is compatible with the report that these 2 areas code intrinsic and extrinsic object properties relevant for grasping (Monaco et al. 2015). Also, coding of object size for grasping actions was previously demonstrated in the IPL (Konen and Kastner 2008; Cavina-Pratesi et al. 2010; Monaco et al. 2010). Actually, the IPLv in our study overlaps highly with the anterior intraparietal area, which is implicated in the computation of grasp-relevant dimensions of objects in conjunction with object size (Monaco et al. 2014). Interestingly, we found that PMv discriminated kinematics but not targets/goals, challenging the suggestion that PMv encodes goals of actions (Rizzolatti and Sinigaglia 2010; Rizzolatti et al. 2014). Our finding that the right-TPj is informed about dissimilarities in both kinematics and target/goal of the observed action is novel and indicates that this region may play a central role in enabling the observer to understand the actor's intention. This finding complements previous reports that the right-TPj is involved in theory of mind (Corbetta et al. 2008; Young et al. 2010; Krall et al. 2015). Overall, our results are in agreement with reports that motor responses during action observation are sensitive to the identity of the target (Ruggiero and Catmur 2018) and to the properties of the object to be-acted-upon (Craighero et al. 2008, 2014). According to the "affordance-matching hypothesis," the object/target offers an object-based view of action understanding. It offers the knowledge of what an object is for and how it is handled, which is the framework for action recognition (Bach et al. 2014).

In summary, areas engaged in action observation are informed about dissimilarities of movement kinematics and/or target identity, and this information may be used for action elucidation.

### Semantic versus Pragmatic Representations of Actions

First, our finding that aimless movements, in the absence of any target/goal, activate classical areas housing mirror neurons contradicts the dogma that mirror neuron areas provide a semantic (high-level intentional) representation of goal-directed actions and suggests that action kinematics, encoded in the action-observation network, plays a crucial role. Second, given that the premotor and parietal areas detect differences in movement kinematics, and kinematics is associated with intention discrimination, we could imply that areas with mirror neurons are associated with action understanding. Nevertheless, there is a big difference between "areas coding intentions," that is, the semantic/abstract representation of actions, and "areas coding kinematics," that is, the pragmatic/concrete sensorimotor representation of action, and therefore are indirectly associated with intentions and action understanding. Identifying low-level representations of movement kinematics (movement pragmatics) with high-level abstract representations of intention (action semantics) is scientifically indefensible.

Overall, our finding that components of the action observation network are informed about differences in movement kinematics and target identity (action pragmatics) suggests that both contextual and kinematic information, processed in the observer's brain, contribute to intention ascription to the actor. These findings complement previous reports (Cook et al. 2014; Catmur 2015) that mirror neurons are involved in low-level processes of action perception and not in high-level intention understanding as originally proposed by the direct perception account (Rizzolatti and Sinigaglia 2007; Rizzolatti and Fogassi 2014). The question is how could movement kinematics combine with contextual cues, such as the target identity, in the recognition of others' actions? Interestingly, it has been suggested that before movement onset, the intention is estimated from the contextual cue (target/goal) whereas during movement, unfolding information specified in kinematics overrides the initial target-based representation of intention (Ansuini et al. 2015).

## Conclusions

All in all, until recently we had experimental evidence that an overt action (action execution) is mentally simulated during the practice of its covert equivalents (action observation and motor imagery). We argued that we decode the actions of others by activating our own action system off-line, supporting internal rehearsal of the observed actions (Simos et al. 2017; Savaki and Raos 2019), which is consistent with the simulation theory (Gordon 1986; Heal 1986). The present finding that areas associated with action observation are affected by movement kinematics and target/goal identity suggests a causal rather than epiphenomenal involvement of the simulated network in action observation and therefore in motor cognition. Indeed, if action understanding was based on higher cognitive functions and not on action simulation, the discrimination of kinematics and targets by the action observation network would be unnecessary. In other words, discrimination of movement kinematics and target/goal identity by areas engaged in action observation supports the notion that the mental simulation of action during its observation serves action understanding. Our findings question motor theories of action concept processing and are in agreement with the theory of motor cognition (Barsalou 1999, 2008; Barsalou et al. 2003), providing further support to the notion that motor cognition is embodied and modal (Savaki and Raos 2019).

## Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

## Funding

Hellenic Foundation for Research and Innovation (H.F.R.I.) under the "First Call for H.F.R.I. Research Projects to support faculty members and researchers and the procurement of high-cost research equipment grant" (Project Number: 1435).

## Notes

We thank Vassilis Raos for constructive comments and Emmanouela Kosteletou-Kassotaki for technical support.
*Conflict of Interest:* None declared.

## References

Aglioti SM, Cesari P, Romani M, Urgesi C. 2008. Action anticipation and motor resonance in elite basketball players. *Nat Neurosci*. 11:1109–1116.

Amiez C, Petrides M. 2009. Anatomical organization of the eye fields in the human and non-human primate frontal cortex. *Prog Neurobiol*. 89:220–230.

Agosta S, Battelli L, Casile A. 2016. Human movements and abstract motion displays activate different processes in the observer's motor system. *Neuroimage*. 130:184–193.

Ansuini C, Cavallo A, Bertone C, Becchio C. 2014. The visible face of intention: why kinematics matters. *Front Psychol*. 5:815.

Ansuini C, Cavallo A, Bertone C, Becchio C. 2015. Intentions in the brain. *Neuroscientist*. 21:126–135.

Ansuini C, Cavallo A, Koul A, D'Ausilio A, Taverna L, Becchio C. 2016. Grasping others' movements: rapid discrimination of object size from observed hand movements. *J Exp Psychol Hum Percept Perform*. 42:918–929.

Arzy S, Thut G, Mohr C, Michel CM, Blanke O. 2006. Neural basis of embodiment: distinct contributions of temporoparietal junction and extrastriate body area. *J Neurosci*. 26:8074–8081.

Bach P, Nicholson T, Hudson M. 2014. The affordance-matching hypothesis: how objects guide action understanding and prediction. *Front Hum Neurosci*. 8:254.

Barany DA, Della-Maggiore V, Viswanathan S, Cieslak M, Grafton ST. 2014. Feature interactions enable decoding of sensorimotor transformations for goal-directed movement. *J Neurosci*. 34:6860–6873.

Barsalou LW. 1999. Perceptual symbol systems. *Behav Brain Sci*. 22:577–609.

Barsalou LW. 2008. Grounded cognition. *Annu Rev Psychol*. 59:617–645.

Barsalou LW, Kyle Simmons W, Barbey AK, Wilson CD. 2003. Grounding conceptual knowledge in modality-specific systems. *Trends Cogn Sci*. 7:84–91.

Becchio C, Cavallo A, Begliomini C, Sartori L, Feltrin G, Castiello U. 2012. Social grasping: from mirroring to mentalizing. *Neuroimage*. 61:240–248.

Becchio C, Sartori L, Bulgheroni M, Castiello U. 2008. The case of Dr. Jekyll and Mr. Hyde: a kinematic study on social intention. *Conscious Cogn*. 17:557–564.

Blanke O, Ionta S, Fornari E, Mohr C, Maeder P. 2010. Mental imagery for full and upper human bodies: common right hemisphere activations and distinct extrastriate activations. *Brain Topogr*. 23:321–332.

Bonini L, Rozzi S, Serventi FU, Simone L, Ferrari PF, Fogassi L. 2010. Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb Cortex*. 20:1372–1385.

Bridge H, Clare S, Krug K. 2014. Delineating extrastriate visual area MT(V5) using cortical myeloarchitecture. *Neuroimage*. 93(Pt 2):231–236.

Buccino G, Binkofski F, Fink GR, Fadiga L, Fogassi L, Gallese V, Seitz RJ, Zilles K, Rizzolatti G, Freund HJ. 2001. Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci*. 13:400–404.

Caggiano V, Fogassi L, Rizzolatti G, Casile A, Giese MA, Thier P. 2012. Mirror neurons encode the subjective value of an observed action. *Proc Natl Acad Sci U S A*. 109:11848–11853.

Caggiano V, Fogassi L, Rizzolatti G, Pomper JK, Thier P, Giese MA, Casile A. 2011. View-based encoding of actions in mirror neurons of area F5 in macaque premotor cortex. *Curr Biol*. 21:144–148.

Caggiano V, Fogassi L, Rizzolatti G, Thier P, Casile A. 2009. Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science*. 324:403–406.

Casile A, Dayan E, Caggiano V, Hendler T, Flash T, Giese MA. 2010. Neuronal encoding of human kinematic invariants during action observation. *Cereb Cortex*. 20:1647–1655.

Caspers S, Zilles K, Laird AR, Eickhoff SB. 2010. ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*. 50:1148–1167.

Catmur C. 2015. Understanding intentions from actions: direct perception, inference, and the roles of mirror and mentalizing systems. *Conscious Cogn*. 36:426–433.

Cavallo AKA, Ansuini C, Capozzi F, Becchio C. 2016. Decoding intentions from movement kinematic. *Sci Rep*. 6:37036.

Cavina-Pratesi C, Monaco S, Fattori P, Galletti C, McAdam TD, Quinlan DJ, Goodale MA, Culham JC. 2010. Functional magnetic resonance imaging reveals the neural substrates of arm transport and grip formation in reach-to-grasp actions in humans. *J Neurosci*. 30:10306–10323.

Cook R, Bird G, Catmur C, Press C, Heyes C. 2014. Mirror neurons: from origin to function. *Behav Brain Sci*. 37:177–192.

Corbetta M, Patel G, Shulman GL. 2008. The reorienting system of the human brain: from environment to theory of mind. *Neuron*. 58:306–324.

Craighero L, Bonetti F, Massarenti L, Canto R, Fabbri Destro M, Fadiga L. 2008. Temporal prediction of touch instant during observation of human and robot grasping. *Brain Res Bull*. 75:770–774.

Craighero L, Zorzi V, Canto R, Franca M. 2014. Same kinematics but different objects during action observation: detection times and motor evoked potentials. *Vis Cogn*. 22:653–671.

Csibra G. 2007. Action mirroring and action understanding: an alternative account. In: Haggard P, Rosetti Y, Kawato M, editors. *Sensorimotor foundations of higher cognition. Attention and performance*. Oxford: Oxford University Press, pp. 453–459.

Davare M, Zenon A, Desmurget M, Olivier E. 2015. Dissociable contribution of the parietal and frontal cortex to coding movement direction and amplitude. *Front Hum Neurosci*. 9:241.

Decety J, Sommerville JA. 2003. Shared representations between self and other: a social cognitive neuroscience view. *Trends Cogn Sci*. 7:527–533.

Di Dio C, Di Cesare G, Higuchi S, Roberts N, Vogt S, Rizzolatti G. 2013. The neural correlates of velocity processing during the observation of a biological effector in the parietal and premotor cortex. *Neuroimage*. 64:425–436.

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

Eickhoff SB, Stephan KE, Mohlberg H, Grefkes C, Fink GR, Amunts K, Zilles K. 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*. 25:1325–1335.

Engel A, Burke M, Fiehler K, Bien S, Rosler F. 2008. How moving objects become animated: the human mirror neuron system assimilates non-biological movement patterns. *Soc Neurosci*. 3:368–387.

Fabbri S, Caramazza A, Lingnau A. 2010. Tuning curves for movement direction in the human visuomotor system. *J Neurosci*. 30:13488–13498.

Fabbri S, Strnad L, Caramazza A, Lingnau A. 2014. Overlapping representations for grip type and reach direction. *Neuroimage*. 94:138–146.

Ferri S, Kolster H, Jastorff J, Orban GA. 2013. The overlap of the EBA and the MT/V5 cluster. *Neuroimage*. 66:412–425.

Filimon F, Nelson JD, Hagler DJ, Sereno MI. 2007. Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage*. 37:1315–1328.

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

Fogassi L, Gallese V, Buccino G, Craighero L, Fadiga L, Rizzolatti G. 2001. Cortical mechanism for the visual guidance of hand grasping movements in the monkey: a reversible inactivation study. *Brain*. 124:571–586.

Friston K, Holmes A, Worsley K, Poline J, Frith C, Frackowiak R. 1995. Statistical parametric maps in functional imaging: a general linear approach. *Hum Brain Mapp*. 2:189–210.

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

Gazzola V, Keysers C. 2009. The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cereb Cortex*. 19:1239–1255.

Georgiou I, Becchio C, Glover S, Castiello U. 2007. Different action patterns for cooperative and competitive behaviour. *Cognition*. 102:415–433.

Georgopoulos AP. 1991. Higher order motor control. *Ann Rev Neurosci*. 14:361–377.

Georgopoulos AP. 2003. Modular organization of directionally tuned cells in the motor cortex: is there a short-range order? *Proc Natl Acad Sci*. 100:12474–12479.

Georgopoulos AP, Schwartz AB, Kettner RE. 1986. Neuronal population coding of movement direction. *Science*. 233:1416–1419.

Gordon RM. 1986. Folk psychology as simulation. *Mind and Language*. 1:158–171.

Grezes J, Decety J. 2001. Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum Brain Mapp*. 12:1–19.

Hamilton AF, Joyce DW, Flanagan JR, Frith CD, Wolpert DM. 2007. Kinematic cues in perceptual weight judgement and their origins in box lifting. *Psychol Res*. 71:13–21.

Hardwick RM, Caspers S, Eickhoff SB, Swinnen SP. 2018. Neural correlates of action: comparing meta-analyses of imagery, observation, and execution. *Neurosci Biobehav Rev*. 94:31–44.

Heal J. 1986. *Replication and functionalism*. Cambridge: Cambridge University Press.

Indovina I, Sanes JN. 2001. On somatotopic representation centers for finger movements in human primary motor cortex and supplementary motor area. *Neuroimage*. 13:1027–1034.

Jeannerod M. 2004. Visual and action cues contribute to the self-other distinction. *Nat Neurosci*. 7:422–423.

Keysers C, Wicker B, Gazzola V, Anton JL, Fogassi L, Gallese V. 2004. A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*. 42:335–346.

Konen CS, Kastner S. 2008. Two hierarchically organized neural systems for object information in human visual cortex. *Nat Neurosci*. 11:224–231.

Koul A, Cavallo A, Cauda F, Costa T, Diano M, Pontil M, Becchio C. 2018. Action observation areas represent intentions from subtle kinematic features. *Cereb Cortex*. 28:2647–2654.

Krall TSC, Rottschy C, Konrad K. 2015. The role of the right temporoparietal junction in attention and social interaction as revealed by ALE meta-analysis. *Brain Struct Funct*. 220: 587–604.

Krishnan-Barman S, Forbes PAG, Hamilton AFC. 2017. How can the study of action kinematics inform our understanding of human social interaction? *Neuropsychologia*. 105:101–110.

Lotze M, Erb M, Flor H, Huelsmann E, Godde B, Grodd W. 2000. fMRI evaluation of somatotopic representation in human primary motor cortex. *Neuroimage*. 11:473–481.

Maeda K, Ishida H, Nakajima K, Inase M, Murata A. 2015. Functional properties of parietal hand manipulation-related neurons and mirror neurons responding to vision of own hand action. *J Cogn Neurosci*. 27:560–572.

Malfait N, Valyear KF, Culham JC, Anton J-L, Brown L, Gribble PL. 2009. fMRI activation during observation of others' reach errors. *J Cogn Neurosci*. 22:1493–1503.

Malikovic A, Amunts K, Schleicher A, Mohlberg H, Eickhoff SB, Wilms M, Palomero-Gallagher N, Armstrong E, Zilles K. 2007. Cytoarchitectonic analysis of the human extrastriate cortex in the region of V5/MT+: a probabilistic, stereotaxic map of area hOc5. *Cereb Cortex*. 17:562–574.

Manera V, Becchio C, Cavallo A, Sartori L, Castiello U. 2011. Cooperation or competition? Discriminating between social intentions by observing prehensile movements. *Exp Brain Res*. 211:547–556.

Marteniuk RG, MacKenzie CL, Jeannerod M, Athenes S, Dugas C. 1987. Constraints on human arm movement trajectories. *Can J Psychol*. 41:365–378.

Mayka MA, Corcos DM, Leurgans SE, Vaillancourt DE. 2006. Three-dimensional locations and boundaries of motor and premotor cortices as defined by functional brain imaging: a meta-analysis. *Neuroimage*. 31:1453–1474.

McAleer P, Pollick FE, Love SA, Crabbe F, Zacks JM. 2014. The role of kinematics in cortical regions for continuous human motion perception. *Cogn Affect Behav Neurosci*. 14:307–318.

Molenberghs P, Cunnington R, Mattingley JB. 2012. Brain regions with mirror properties: a meta-analysis of 125 human fMRI studies. *Neurosci Biobehav Rev*. 36:341–349.

Monaco S, Cavina-Pratesi C, Sedda A, Fattori P, Galletti C, Culham JC. 2011. Functional magnetic resonance adaptation reveals the involvement of the dorsomedial stream in hand orientation for grasping. *J Neurophysiol*. 106:2248–2263.

Monaco S, Chen Y, Medendorp WP, Crawford JD, Fiehler K, Henriques DY. 2014. Functional magnetic resonance imaging adaptation reveals the cortical networks for processing grasp-relevant object properties. *Cereb Cortex*. 24:1540–1554.

Monaco S, Kroliczak G, Quinlan DJ, Fattori P, Galletti C, Goodale MA, Culham JC. 2010. Contribution of visual and proprioceptive information to the precision of reaching movements. *Exp Brain Res*. 202:15–32.

Monaco S, Sedda A, Cavina-Pratesi C, Culham JC. 2015. Neural correlates of object size and object location during grasping actions. *Eur J Neurosci*. 41:454–465.

Myers A, Sowden PT. 2008. Your hand or mine? The extrastriate body area. *Neuroimage*. 42:1669–1677.

Naish KR, Reader AT, Houston-Price C, Bremner AJ, Holmes NP. 2013. To eat or not to eat? Kinematics and muscle activity of reach-to-grasp movements are influenced by the action goal, but observers do not detect these differences. *Exp Brain Res*. 225:261–275.

Nelissen K, Luppino G, Vanduffel W, Rizzolatti G, Orban GA. 2005. Observing others: multiple action representation in the frontal lobe. *Science*. 310:332–336.

Papadourakis V, Raos V. 2017. Evidence for the representation of movement kinematics in the discharge of F5 mirror neurons during the observation of transitive and intransitive actions. *J Neurophysiol*. 118:3215–3229.

Peelen MV, Downing PE. 2007. The neural basis of visual body perception. *Nat Rev Neurosci*. 8:636–648.

Perrett DI, Harries MH, Bevan R, Thomas S, Benson PJ, Mistlin AJ. 1989. Frameworks of analysis for the neural representation of animate objects and actions. *J Exp Biol*. 146:87–113.

Petrides M. 1994a. Frontal lobes and behaviour. *Curr Opin Neurobiol*. 4:207–211.

Petrides M. 1994b. Frontal lobes and working memory: evidence from investigations of the effects of cortical excisions in nonhuman primates. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*. Amsterdam: Elsevier, pp. 59–82.

Petrides M. 1996. Specialized systems for the processing of mnemonic information within the primate frontal cortex. *Philos Trans R Soc Lond B Biol Sci*. 351:1455–1461.

Petrides M. 2005. Lateral prefrontal cortex: architectonic and functional organization. *Philos Trans R Soc Lond B Biol Sci*. 360:781–795.

Petrides M, Pandya DN. 1984. Projections to the frontal cortex from the posterior parietal region in the rhesus monkey. *J Comp Neurol*. 228:105–116.

Petrides M, Pandya DN. 1994. Comparative architectonic analysis of the human and the macaque frontal cortex. In: Boller F, Grafman J, editors. *Handbook of neuropsychology*. Amsterdam: Elsevier, pp. 17–58.

Prinz W. 2014. Action representation: crosstalk between semantics and pragmatics. *Neuropsychologia*. 55:51–56.

Raos V, Kilintari M, Savaki HE. 2014. Viewing a forelimb induces widespread cortical activations. *Neuroimage*. 89:122–142.

Rizzolatti G, Cattaneo L, Fabbri-Destro M, Rozzi S. 2014. Cortical mechanisms underlying the organization of goal-directed actions and mirror neuron-based action understanding. *Physiol Rev*. 94:655–706.

Rizzolatti G, Fadiga L, Gallese V, Fogassi L. 1996. Premotor cortex and the recognition of motor actions. *Cogn Brain Res*. 3:131–141.

Rizzolatti G, Fogassi L. 2014. The mirror mechanism: recent findings and perspectives. *Philos Trans R Soc B Biol Sci*. 369:20130420.

Rizzolatti G, Sinigaglia C. 2007. Mirror neurons and motor intentionality. *Funct Neurol*. 22:205–210.

Rizzolatti G, Sinigaglia C. 2010. The functional role of the parieto-frontal mirror circuit: interpretations and misinterpretations. *Nat Rev Neurosci*. 11:264–274.

Rizzolatti G, Sinigaglia C. 2016. The mirror mechanism: a basic principle of brain function. *Nat Rev Neurosci*. 17:757–765.

Romo R, de Lafuente V. 2013. Conversion of sensory signals into perceptual decisions. *Prog Neurobiol*. 103:41–75.

Romo R, Hernandez A, Zainos A, Lemus L, Brody CD. 2002. Neuronal correlates of decision-making in secondary somatosensory cortex. *Nat Neurosci*. 5:1217–1225.

Romo R, Lemus L, de Lafuente V. 2012. Sense, memory, and decision-making in the somatosensory cortical network. *Curr Opin Neurobiol*. 22:914–919.

Ruggiero M, Catmur C. 2018. Mirror neurons and intention understanding: dissociating the contribution of object type and intention to mirror responses using electromyography. *Psychophysiology*. 55:e13061.

Sakreida K, Schubotz RI, Wolfensteller U, von Cramon DY. 2005. Motion class dependency in observers' motor areas revealed by functional magnetic resonance imaging. *J Neurosci*. 25:1335–1342.

Sartori L, Becchio C, Bara BG, Castiello U. 2009. Does the intention to communicate affect action kinematics? *Conscious Cogn*. 18:766–772.

Sartori L, Becchio C, Castiello U. 2011. Cues to intention: the role of movement information. *Cognition*. 119:242–252.

Savaki H. 2010. How do we understand the actions of others? By mental simulation, NOT mirroring. *Cognitive Critique*. 2:99–140.

Savaki HE, Raos V. 2019. Action perception and motor imagery: mental practice of action. *Prog Neurobiol*. 175:107–125.

Saygin AP. 2007. Superior temporal and premotor brain areas necessary for biological motion perception. *Brain*. 130:2452–2461.

Simos PG, Kavroulakis E, Maris T, Papadaki E, Boursianis T, Kalaitzakis G, Savaki HE. 2017. Neural foundations of overt and covert actions. *Neuroimage*. 152:482–496.

Sirigu A, Cohen L, Duhamel JR, Pillon B, Dubois B, Agid Y, Pierrot-Deseilligny C. 1995. Congruent unilateral impairments for real and imagined hand movements. *Neuroreport*. 6: 997–1001.

Sirigu A, Daprati E, Pradat-Diehl P, Franck N, Jeannerod M. 1999. Perception of self-generated movement following left parietal lesion. *Brain*. 122:1867–1874.

Sirigu A, Duhamel JR, Cohen L, Pillon B, Dubois B, Agid Y. 1996. The mental representation of hand movements after parietal cortex damage. *Science*. 273:1564–1568.

Slepian ML, Young SG, Rutchick AM, Ambady N. 2013. Quality of professional players' poker hands is perceived accurately from arm motions. *Psychol Sci*. 24:2335–2338.

Slotnick SD. 2017. Cluster success: fMRI inferences for spatial extent have acceptable false-positive rates. *Cogn Neurosci*. 8:150–155.

Slotnick SD, Moo LR, Segal JB, Hart J Jr. 2003. Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Brain Res Cogn Brain Res*. 17:75–82.

Sowden S, Catmur C. 2015. The role of the right temporoparietal junction in the control of imitation. *Cereb Cortex*. 25:1107–1113.

Spiridon M, Fischl B, Kanwisher N. 2006. Location and spatial profile of category-specific regions in human extrastriate cortex. *Hum Brain Mapp*. 27:77–89.

Tomaiuolo F, MacDonald JD, Caramanos Z, Posner G, Chiavaras M, Evans AC, Petrides M. 1999. Morphology, morphometry and probability mapping of the pars opercularis of the inferior frontal gyrus: an in vivo MRI analysis. *Eur J Neurosci*. 11:3033–3046.

Umilta MA, Kohler E, Gallese V, Fogassi L, Fadiga L, Keysers C, Rizzolatti G. 2001. I know what you are doing. A neurophysiological study. *Neuron*. 31:155–165.

Vaina LM, Solomon J, Chowdhury S, Sinha P, Belliveau JW. 2001. Functional neuroanatomy of biological motion perception in humans. *Proc Natl Acad Sci U S A*. 98:11656–11661.

Van Overwalle F, Baetens K. 2009. Understanding others' actions and goals by mirror and mentalizing systems: a meta-analysis. *Neuroimage*. 48:564–584.

Villarreal M, Fridman EA, Amengual A, Falasco G, Gerscovich ER, Ulloa ER, Leiguarda RC. 2008. The neural substrate of gesture recognition. *Neuropsychologia*. 46:2371–2382.

Weiner KS, Grill-Spector K. 2013. Neural representations of faces and limbs neighbor in human high-level visual cortex: evidence for a new organization principle. *Psychol Res*. 77: 74–97.

Young L, Dodell-Feder D, Saxe R. 2010. What gets the attention of the temporo-parietal junction? An fMRI investigation of attention and theory of mind. *Neuropsychologia*. 48: 2658–2664.