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ORIGINAL ARTICLE

# Constructing Visual Perception of Body Movement with the Motor Cortex

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## Abstract

The human brain readily perceives fluent movement from static input. Using functional magnetic resonance imaging, we investigated brain mechanisms that mediate fluent apparent biological motion (ABM) perception from sequences of body postures. We presented body and nonbody stimuli varying in objective sequence duration and fluency of apparent movement. Three body postures were ordered to produce a fluent (ABC) or a nonfluent (ACB) apparent movement. This enabled us to identify brain areas involved in the perceptual reconstruction of body movement from identical lower-level static input. Participants judged the duration of a rectangle containing body/nonbody sequences, as an implicit measure of movement fluency. For body stimuli, fluent apparent motion sequences produced subjectively longer durations than nonfluent sequences of the same objective duration. This difference was reduced for nonbody stimuli. This body-specific bias in duration perception was associated with increased blood oxygen level-dependent responses in the primary (M1) and supplementary motor areas. Moreover, fluent ABM was associated with increased functional connectivity between M1/SMA and right fusiform body area. We show that perceptual reconstruction of fluent movement from static body postures does not merely enlist areas traditionally associated with visual body processing, but involves cooperative recruitment of motor areas, consistent with a "motor way of seeing".

**Key words:** biological motion, EBA, FBA, motor resonance, M1, visual body perception

## Introduction

Seeing and understanding the movements of others lies at the basis of social interactions. Vivid perception of body movement can result from purely static input, producing representational momentum (Freyd 1983; Verfaillie and Daems 2002), implied motion (Kourtzi and Shiffrar 1999; Kourtzi and Kanwisher 2000) and apparent motion (Shiffrar and Freyd 1990, 1993; Orgs et al. 2011a, 2011b, 2013a, 2013b) for body postures. In apparent biological motion (ABM), alternating between static images of initial and final positions of a movement induces perception of a plausible movement as long as the stimulus onset asynchrony (SOA) between the images is consistent with actual movement duration (Shiffrar

and Freyd 1990, 1993; Grosjean et al. 2007). In the present study, we have investigated the neural mechanisms of fluent ABM perception using functional magnetic resonance imaging (fMRI).

Previous research suggests 2 potential brain mechanisms: On one view seeing ABM would be related only to visual perception of the body. Neurons in the human superior temporal sulcus (Puce and Perrett 2003; Blake and Shiffrar 2007) and extra-striate visual areas are specifically tuned to human bodies (fusiform body area, FBA) or body parts (extra-striate body area, EBA). Whereas EBA and FBA are primarily involved in processing static body form (Peelen and Downing 2007; Downing and Peelen 2011; Vangeneugden et al. 2014), the posterior part of the superior temporal sulcus (pSTS) is sensitive to whole-body kinematics (Puce and Perrett 2003; Blake and Shiffrar 2007; Grosbras, Beaton and Eickhoff 2012). Thus, sequence-selective and body-specific neurons in these areas might receive sufficient bottom-up input to produce fluent ABM perception, complementing the missing frames that are absent in the ABM stimulus (Giese and Poggio 2003; Jellema and Perrett 2003; Barraclough et al. 2006).

On an alternative view, reconstructing dynamic human movement from a sequence of static body postures could involve concurrent activity of both motor and visual brain areas. The human "mirror neuron system" (MNS), centered on parietal and premotor cortices, shows similar responses when observing and executing specific motor actions (Gazzola and Keysers 2009; Rizzolatti and Sinigaglia 2010), and could potentially contribute to this process. Motor activations during the observation of others' actions indeed contribute to action understanding, action prediction, and imitation learning (Kohler et al. 2002; Buccino et al. 2004; Fadiga et al. 2005; Kilner et al. 2007; Heyes 2011). In the case of ABM perception, such "motor resonance" (Fadiga et al. 1995, 2005) might compensate for the absence of bottom-up movement kinematics (Stevens et al. 2000; Grosjean, Shiffrar and Knoblich 2007), when the stimulus itself contains no motion information. Recent imaging studies suggest this kind of resonant activity extends widely in the brain, beyond the classical MNS. Thus, activity in occipito-temporal cortex (OTC) is modulated by performing unseen actions (Astafiev et al. 2004; Orlov et al. 2010) or by object affordances (Bracci and Peelen 2013). These findings show that brain areas traditionally associated primarily with visual functions also participate in motor processing, and may even be a functional part of the human MNS (Oosterhof et al. 2013). Such co-operations between visual and motor areas might conceivably be bidirectional, with motor output areas also contributing to visual perception of human movement. In the case of ABM, motor areas might help to reconstruct fluent body movement by generating movement-related information, despite impoverished visual stimulation (Grosjean et al. 2007; Schutz-Bosbach and Prinz 2007).

Thus, the 2 views differ principally regarding whether perception of body movement does or does not make reference to the neural mechanisms for controlling movement, notably the primary motor areas.

Only few imaging studies have specifically aimed to identify neural correlates of ABM perception. Using positron emission tomography (PET), Stevens et al. (2000) found that seeing feasible apparent movement paths correlated with activity in primary motor cortex. However, it remains unclear how this motor activity relates to the extraction of visual body features in areas such as the pSTS, EBA, or FBA. Interestingly, Downing et al. (2006) showed that incoherently ordered sequences of body postures were associated with greater activity in EBA than coherently ordered sequences, whereas the reverse effect was observed in pSTS. Importantly, however, this study did not include any perceptual measure of apparent movement.

To elucidate the neural mechanism of seeing ABM, we used duration discrimination of an irrelevant stimulus as an implicit measure of perceiving fluent movement. Use of such an implicit measure minimizes any possible influence of explicit movement imagery, while providing a quantitative, continuous measure of the vividness of the apparent motion percept: We have previously shown that seeing apparent movement induced body-specific distortions of perceived time. Perceived duration of a rectangle containing apparent motion sequences increased with the fluency of the apparent movement, as implied by the order of 3 consecutive body postures (Orgs et al. 2011a, 2011b, 2013a). Seeing ABM is thus associated with body-specific and sequence-selective biases in perceived temporal duration. This suggests that a static posture sequence can in fact be perceived as an extended dynamic event, rather than a series of postures. Importantly, these manipulations of movement fluency involved only a reordering of the sequence of the same 3 body postures. These manipulations biased the perceived duration of 2 stimulus sequences with "objectively" identical presentation timing, and containing identical static postural information (Orgs et al. 2011a, 2011b, 2013a). In the present study, measuring brain activity while viewing such stimuli allowed us to investigate to what extent "visual" and "motor" cortices were involved when reconstructing percepts of fluent body movement from static body stimuli.

Accordingly, the present study aims to test 2 main hypotheses: Firstly, we assessed whether temporal biases induced by fluent ABM perception correlated with increased activity in motor cortex, in perceptual body/movement areas (pSTS/EBA/FBA) or both. If motor areas participate in ABM perception, body stimuli that generate a perceptual experience of movement should recruit the motor system more than nonbody stimuli, and more than body stimuli that do not generate perceptual experiences of fluent movement. Secondly, if the reconstruction of visual body movement from static body posture requires communication of the "visual" and the "motor" areas, and not just a simple coactivation of the 2, it should be reflected as increased functional connectivity between the motor cortex and pSTS, EBA, or FBA during the subjective experience of ABM, but not when viewing control stimuli that do not produce ABM.

## Materials and Methods

### Participants

We collected data from 24 participants (mean age: 25.7; range: 20–40, 14 male). All participants were right-handed as assessed by the Edinburgh handedness inventory (Oldfield 1971) and reported normal or corrected to normal vision. All participants gave written informed consent. The study was performed in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and approved by the ethics committee of the University Hospital Cologne.

### Stimuli and Experimental Design

Five abstract dance movements were professionally choreographed and captured digitally (for a full list of stimuli, see Supplementary Material and Orgs et al. 2011a). Three gray-scale pictures were selected representing initial (A), intermediate (B), and final postures (C) of each dance movement. Any arrangement of these 3 postures produced a feasible apparent movement.

From each dance movement, we created 4 body posture triplets that produced either a fluent ABM sequence (ABC/CBA) or a nonfluent ABM sequence. Nonfluent movements were created by swapping the intermediate and final postures (ACB/CAB), producing a movement direction reversal (Fig. 1A). Thus, fluent and nonfluent apparent movements were created from 3 identical static body postures and therefore were fully matched for lower-level visual features. To test for body specificity of apparent motion, we created control stimuli by degrading spatial resolution of the body postures, so that overall human form was no longer recognizable (nonbody stimuli, Fig. 1A). Overall stimulus size remained the same (see Orgs et al. 2008; Calvo-Merino et al. 2010; Orgs et al. 2011a, 2011b for a similar approach). Furthermore, the SOA of the body posture triplets was systematically varied [short SOA (250 ms) vs. long SOA (350 ms), see Fig. 1A]. Both SOAs are suitable for producing body-specific temporal

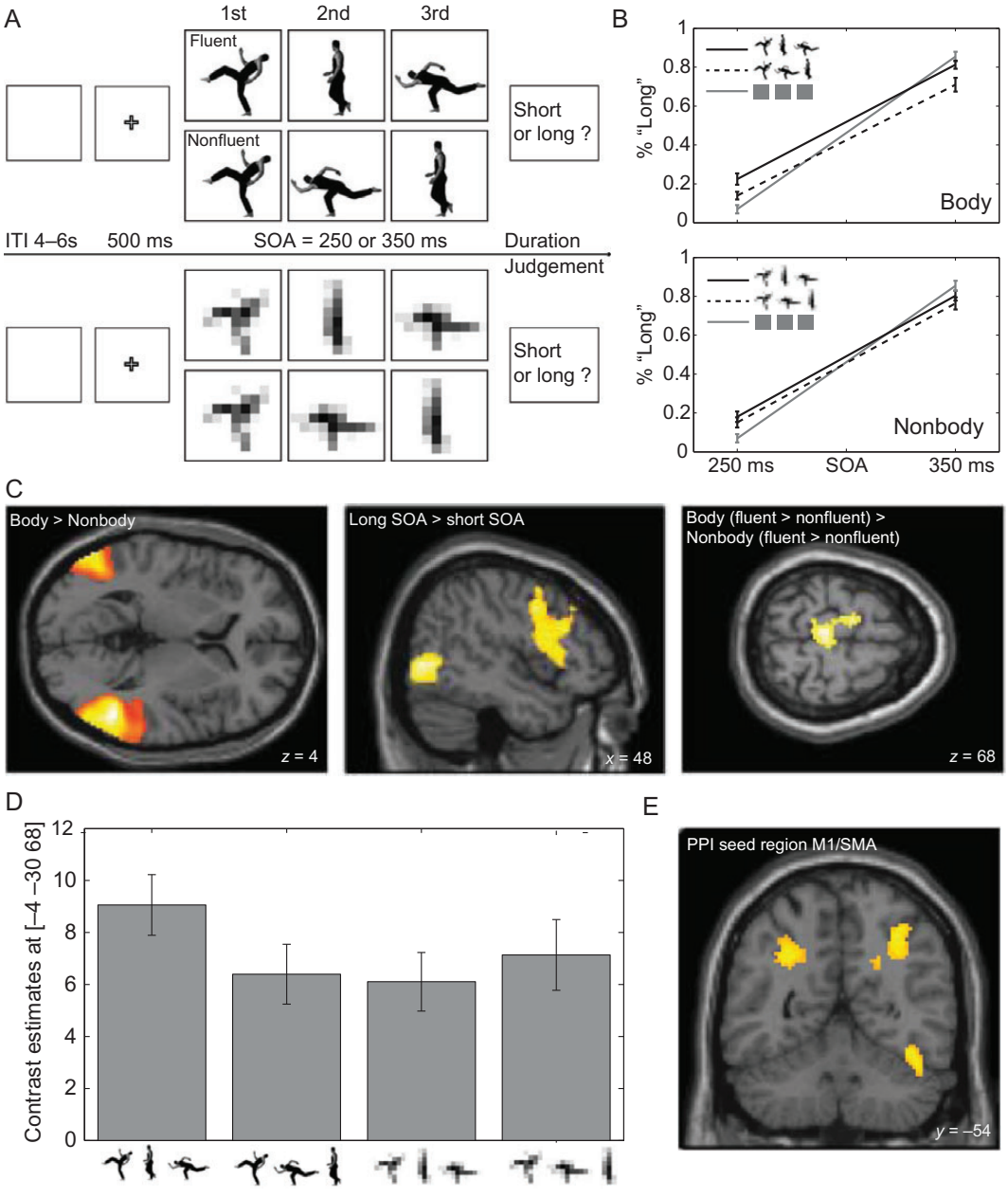


**Figure 1.** Rearranging 3 successive postures produces either fluent or nonfluent ABM (*A*) that induces body-specific distortions in perceived duration (*B*). (*C*) Results of the GLM analysis are depicted on the standard MNI-template brain provided by SPM: Bilateral activations in the middle temporal gyrus (EBA) extending into the pSTS were revealed by the main effect of body versus nonbody trials; the main effect of long versus short SOA trials yielded activations in visual areas and the inferior frontal gyrus; the interaction contrast associated with the body-specific temporal bias for fluent versus nonfluent ABM led to activations in a motor cluster comprising medial primary motor cortex (M1) and posterior SMA. All depicted activations are significant at $P < 0.05$, corrected for multiple comparisons at the cluster level with a height threshold at the voxel level of $P < 0.005$, uncorrected (see Table 1). (*D*) $\beta$ estimates (as revealed by the interaction term) in medial M1 for fluent versus nonfluent ABM sequences of body (left bars) and nonbody (right bars) stimuli. (*E*) A body-specific PPI analysis revealed that the activity of the medial motor cluster correlated with activity in left parietal cortex and right fusiform gyrus (FBA) for fluent ABM, see Table 3 for MNI coordinates and significances. For display purposes a threshold $P = 0.005$ uncorrected (extent threshold 100 voxels) was used.

biases and are well within the range at which feasible movement paths are perceived (Shiffrar and Freyd 1990, 1993; Stevens et al. 2000; Orgs et al. 2011a, 2011b). Accordingly, the subjective perception of movement fluency was orthogonal to the objective duration of the stimulus sequence (Orgs et al. 2013b). This 2 (body/nonbody) by 2 (short/long SOA) by 2 (fluent/nonfluent ABM) factorial design resulted in 8 different experimental conditions.

Additionally, we included a flicker control condition (3 uniform gray squares instead of the body/nonbody stimuli) at both SOAs that allowed us to compute a behavioral baseline for duration judgments resulting in 10 conditions in total. All experimental stimuli were matched for brightness and contrast.

### Task and Procedure

Participants were instructed to judge the duration of a white rectangle surrounding the body/nonbody stimuli or the uniform gray square in the flicker control condition, body/nonbody stimuli or gray squares were task irrelevant. Trials started with a blank screen (Fig. 1A), displayed for a random interval between 4 and 6 s, followed by the display of a fixation cross for 500 ms. This was followed by the onset of a white rectangle, which contained a sequence of 3 pictures (either body, nonbody, or gray squares), each displayed for 150 ms. Pictures were separated by SOAs of either 250 or 350 ms. The white rectangle surrounded the stimuli and remained visible throughout the picture sequence. Thus, overall duration of the white rectangle was either 950 or 1150 ms. During the next 2 seconds participants were required to make a response ("short" or "long" temporal partition, see below), using their index finger of both hands. Button assignment was counterbalanced across participants, to prevent any possible influence of effector specific motor preparation on our findings.

The task was a temporal partitioning task (Wearden and Ferrara 1995, 1996). In temporal partitioning the duration of a single trial is compared with all other previously experienced durations in the experiment, rather than with specific standard stimulus presented in each trial. Participants judge whether duration of a trial is relatively "short" or "long". The criterion for duration discrimination was established during a practice session prior to scanning: 10 trials displaying the flicker control condition only were presented with the same durations (250 vs. 350 ms SOA) as in the main experiment. Participants were informed that a white rectangle would appear on the screen containing a sequence of 3 smaller gray squares. Their task was to judge the duration of the white rectangle and to ignore the sequence of gray squares it contained. All participants performed the practice repeatedly until they were correct on 80% of all trials. To achieve this performance criterion, participants completed on average 2 practice sessions. After completion of the practice, participants were informed that for the main experiment the white square would contain different sets of images in addition to the gray square, including body postures. The task would remain identical though; that is, to judge the duration of the white square while ignoring any other images that it might contain and based on the same criterion that was established during the practice session.

In the scanning session, participants completed 3 runs (100 trials per run, 30 trials per condition overall). The order of trials was randomized per block and participant.

### fMRI Data Acquisition

$T_2$*-weighted echo-planar imaging (EPI) images were obtained using a 3-T MRI System (Trio, Siemens, Erlangen, Germany) with blood oxygen level-dependent (BOLD) contrast (matrix size: 64 × 64; voxel size = 3.1 × 3.1 × 3.0 $mm^3$; field of view (FOV) = 200 mm; repetition time = 2200 ms; echo time = 30 ms; flip angle 90°; 36 slices with a slice thickness of 3.0 mm; interslice gap: 0.3 mm). For each participant a total of 1020 functional volumes were collected in 3 scanning sessions. The first 3 EPI volumes of each session were omitted to allow for $T_1$ equilibration effects. The data were preprocessed and analyzed with SPM8 (Wellcome Department of Imaging Neuroscience, London; http://www.fil.ion.ucl.ac.uk/spm). To correct for interscan movement, the images were spatially realigned to the first of the remaining 337 volumes per session and subsequently realigned to the mean of all images. Mean EPI images were then spatially normalized to the Montreal Neurological Institute (MNI) single subject template using the unified segmentation function in SPM8. The normalized images were then spatially smoothed using an 8 mm full-width at half-maximum Gaussian kernel.

Additionally, structural high-resolution MR images were acquired using a standard $T_1$-weighted 3D magnetization prepared rapid gradient echo sequence (matrix size = 256 × 256; voxel size = 1 × 1 × 1 $mm^3$; FOV = 256 mm; repetition time = 2250 ms; echo time = 3.03 ms; flip angle = 15°; inversion time = 300 ms).

### fMRI Data Analysis

For each subject (first-level analysis), we fitted a general linear model (GLM) with the contrasts body/nonbody, short/long SOA, and fluent/nonfluent ABM (8 conditions) as well as the 2 flicker control conditions at both SOAs resulting in 10 conditions in total. Furthermore, the 6 movement regressors from the realignment procedure in SPM were included into the design matrix. At the first level, we computed standard statistical parametric *T*-score maps for all main effects of interest (body vs. nonbody, fluent vs. nonfluent apparent motion, short vs. long SOA) and the interaction effect reflecting a body-specific temporal bias triggered by fluent versus nonfluent ABM sequences (body/fluent > body/nonfluent) > (nonbody/fluent > nonbody/nonfluent) as well as the reverse interaction contrast for nonfluent > fluent ABM. Bold responses were modeled in an event-related design (stimulus duration 0) time-locked to the onset of the first picture of the sequence. For the second-level random effects analysis we computed *T*-contrast images across all subjects for all effects of interests (see Table 1). Whole-brain activations are reported at a significance threshold of $T = 2.8$, i.e., $P < 0.05$, corrected for multiple comparisons at the cluster level with a height threshold at the voxel level of $P < 0.005$, uncorrected.

Additionally, for the body versus nonbody contrast we performed small volume corrections (SVCs), as we predicted greater activity in 3 body-specific visual areas for this contrast. Our predictions were based on a recent meta-analysis (Grosbras et al. 2012) of brain regions showing increased activity for perception of human as compared with nonhuman movement: SVCs were performed for right [50 −68 −2] and left [−44 −74 2] middle temporal gyrus (EBA), right [54 −54 10] and left [−52 −50 4] pSTS, and right [42 −54 −20] and left [-40 −48 −20] fusiform gyrus (FBA). SVCs were based on 8 mm spheres surrounding these coordinates. We further tested the parahippocampal place area (PPA) as an additional higher order visual region that should not display a body-specific response. Coordinates for the PPA were taken from Peelen and Downing (2005). Their Talairach coordinates were converted to MNI space using the mapping procedure by Lacadie et al. (2008) resulting in the coordinates [28 −39 −16] for right PPA and [−25 −44 −16] for left PPA.

**Table 1** Brain regions showing significant relative increases of BOLD response associated with each comparison of interest

| | Hemisphere | Cluster size (voxels) | Max T-value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | x | y | z |
| Body > Nonbody | | | | | | |
| Posterior superior temporal sulcus (pSTS) | R | 3214 | 10.10 | 52 | −54 | 4 |
| Middle temporal gyrus (EBA) | R | | 7.99 | 56 | −68 | 0 |
| Middle temporal gyrus (EBA) | L | 1384 | 7.56 | −56 | −68 | 2 |
| Posterior superior temporal sulcus (pSTS) | L | | 2.97 | −52 | −46 | 12 |
| Nonbody > Body | | | | | | |
| Fusiform gyrus | L | 1557 | 4.57 | −30 | −56 | −18 |
| Middle occipital gyrus | L | | 4.39 | −32 | −84 | 8 |
| Lingual gyrus (V4) | L | | 3.80 | −32 | −84 | −14 |
| Long SOA > Short SOA | | | | | | |
| Inferior occipital gyrus | R | 1561 | 5.29 | 36 | −82 | −2 |
| Middle temporal gyrus (V5) | R | | 5.11 | 46 | −72 | 2 |
| Middle frontal gyrus | R | 2167 | 4.71 | 40 | 4 | 38 |
| Inferior frontal gyrus (Area 44) | R | | 4.01 | 52 | 10 | 16 |
| Fusiform gyrus | L | 1665 | 5.13 | −38 | −58 | −18 |
| Inferior occipital gyrus | L | | 4.87 | −34 | −74 | −8 |
| Interaction 1 (body/fluent > body/nonfluent) > (nonbody/fluent > nonbody/nonfluent): | | | | | | |
| Supplementary motor area (Area 6) | L | 543 | 4.21 | −12 | −20 | 64 |
| | L | | 3.74 | −12 | −10 | 68 |
| Primary motor cortex (Area 4a) | L | | 4.19 | −4 | −30 | 68 |
| Short SOA > Long SOA: n.s. | | | | | | |
| Fluent > nonfluent: n.s. | | | | | | |
| Nonfluent > fluent: n.s. | | | | | | |
| Interaction 2 (body/nonfluent > body/fluent) > (nonbody/nonfluent > nonbody/fluent): n.s. | | | | | | |

For each activation cluster, the coordinates in MNI space are given referring to the maximally activated voxel within an activation cluster as indicated by the highest T-value (additionally, some sub-maxima are provided when clusters extend into neighboring brain regions. All activations are significant at $P < 0.05$ (corrected for multiple comparisons at the cluster level using a height threshold of $P < 0.005$, uncorrected).
SOA, stimulus-onset asynchrony; R, right; L, left; EBA, extra-striate body area; pSTS, posterior superior temporal sulcus; V5, visual area 5.

### Functional Connectivity (PPI Analysis)

We tested whether motor areas that were sensitive to the body-specific temporal bias (Fig. 1C) triggered by ABM showed specific couplings with visual body-specific regions when fluent ABM sequences were presented. For each subject, volumes of interest (12 mm sphere) were extracted based on the individual activation peaks closest to the peak coordinate of the motor cluster derived from the interaction term of the second level analysis ([−12 −20 64], Table 1). A 12 mm sphere was chosen to include both sub peaks (SMA and M1) of the motor cluster (see Table 1). In these "seed" regions, the individual signal was extracted as a physiological time series. To calculate the PPI for body stimuli, the physiological time series was multiplied by a psychological regressor coding for fluent (1) or nonfluent (−1) body posture sequences. The psychological regressor was set to zero for the 4 nonbody and the 2 flicker control conditions, thus correcting for the variance associated with parameters of no interest (Friston et al. 1997; Gitelman et al. 2003). The resulting psycho-physiological interaction (PPI) regressor, in addition to both the physiological and the psychological regressors, were then entered into a first level GLM model that also included the movement regressors. We computed standard parametric T-maps for each subject (PPI regressor = 1, 0 for all other conditions in the design matrix), which were then entered into random effects group analyses. Any brain regions correlated with this regressor will indicate its increased interaction with the motor cluster for the reconstruction of fluent body movement. We computed PPIs across the entire brain (again the significance threshold was set to $T = 2.8$, i.e., $P < 0.05$, corrected for multiple comparisons at the cluster level with a height threshold at the voxel level of $P < 0.005$, uncorrected) and used SVCs (8/12 mm) for predicted increases in connectivity of the motor cluster to the 3 core "target" regions involved in human movement perception (EBA, FBA, and pSTS; see Grosbras et al. 2012) and an additional control area, the PPA based on coordinates from Peelen and Downing (2005).

To account for the body specificity of the above result, we performed the same PPI for the nonbody stimuli. The procedure for the nonbody PPI was identical except that the psychological regressor was set to zero for body and flicker control stimuli, (1) for fluent nonbody and (−1) for nonfluent nonbody picture sequences.

## Results

### Behavioral Data

In line with previous findings (Orgs et al. 2011a, 2011b, 2013b) we observed that fluent apparent motion sequences were associated with subjectively longer durations (of the surrounding white rectangle) than nonfluent sequences [2 (stimulus type) × 2 (motion fluency) × 2 (SOA) ANOVA: $F_{1,22} = 40.7$, $P < 0.0001$, $\eta 2 = 0.65$], see Figure 1B. This temporal bias was body-specific, since it was significantly greater for body than for nonbody stimuli, irrespective of the SOA: The 2-way interaction of stimulus type by motion fluency was significant ($F_{2,22} = 9.3$, $P = 0.006$, $\eta^2 = 0.3$), but not the 3-way interaction stimulus type × motion fluency × SOA ($F_{1,22} = 0.7$, $P = 0.78$, $\eta^2 = 0.003$). Bonferroni-corrected post hoc paired T-tests revealed a highly significant difference between fluent

and nonfluent ABM sequences for body stimuli ($t_{(23)} = 6.3$, $P < 0.0004$), but the corresponding difference for nonbody stimuli just failed to achieve significance ($t_{(23)} = 2.7$, $P = 0.052$). As expected, longer SOAs were associated with significantly more "long" responses (main effect of SOA: ($F_{1,22} = 460.3$, $P < 0.0001$, $\eta 2 = 0.95$). There were no other significant main effects or interactions (all $P > 0.13$).

To assess the influence of nonspecific apparent motion on time perception, we conducted a separate analysis comparing the control flicker condition to both body and nonbody conditions, collapsed across picture order. A 3 (stimulus type: body/nonbody/flicker) × 2 (SOA: 250 ms/350 ms) ANOVA revealed a significant interaction of stimulus type with SOA ($F_{2,44} = 28.9$, $P < 0.001$, $\eta^2 = 0.57$), reflecting greater duration sensitivity for the flickering gray square condition used as control compared with both the body and the nonbody conditions: At the short SOA participants made significantly fewer correct "short" responses in the nonbody/body conditions than in the flicker condition (body: $t_{(23)} = 4.7$, $P < 0.0001$, nonbody: $t_{(23)} = 3.3$, $P < 0.003$; Bonferroni correction: 0.05/6 = 0.0083). Moreover, at the long SOA participants tended to make fewer correct "long" responses in the nonbody/body conditions than in the flicker condition (body: $t_{(23)} = -3.6$, $P < 0.002$; nonbody: $t_{(23)} = -2.4$, $P = 0.026$, n.s.). There were no significant differences between body and nonbody stimuli (short SOA (250 ms): $t_{(23)} = 0.64$, $P = 0.53$, n.s.; long SOA (350 ms): $t_{(23)} = -0.87$, $P = .39$, n. s.). Thus, temporal discrimination performance was similar for both apparent motion conditions (body and nonbody), but was less accurate relative to the flicker control condition. This suggests that perceiving apparent motion for both body and nonbody stimuli impaired temporal discrimination, presumably due to diverting attention away from the primary task that involved duration judgments about the frame surrounding the stimulus sequence. However, such attentional capture due to seeing motion did not differ between body and nonbody stimuli and can therefore not explain the body-specific temporal bias reported here.

## Neural Data

The factorial design enabled us to assess the following 6 main effect contrasts: Body > Nonbody, Nonbody > Body, Long SOA > Short SOA, Short SOA > Long SOA, fluent apparent motion > nonfluent apparent motion, and nonfluent apparent motion > fluent apparent motion. The main focus of the analysis was to assess the neural substrate underlying body-specific fluent (and nonfluent) ABM by computing the respective interaction contrasts: (body/fluent > body/nonfluent) > (nonbody/fluent > nonbody/nonfluent) and (body/nonfluent > body/fluent) > (nonbody/nonfluent > nonbody/fluent); for an overview of the results of all contrasts of interest see Table 1.

Contrasting all body trials with all nonbody trials revealed several clusters of body-specific activations: The whole-brain analysis revealed 2 clusters in right and left middle temporal gyrus (EBA), extending into pSTS (see Fig. 1C and Table 1). SVC analysis revealed similar activations in the middle temporal gyrus and pSTS, but we additionally observed increased activity in the left and right fusiform gyri (FBA) for the main effect of body versus nonbody stimuli (see Table 2). The reverse contrast (nonbody > body) revealed increased activity in the left fusiform gyrus extending into middle occipital and lingual gyrus. Brain regions underlying the processing of objective duration were revealed by the main effects for short and long SOAs. Contrasting all trials containing long SOAs with all trials containing short SOAs revealed 3 significant clusters of activation. These clusters of activation were located in right inferior occipital gyrus extending into middle temporal gyrus, in right middle frontal gyrus extending into inferior frontal gyrus and in left fusiform gyrus extending into inferior occipital gyrus. In contrast, no brain regions were significantly stronger activated in short SOA trials compared with long SOA trials. Moreover, no significant clusters of activation were found when contrasting fluent apparent motion trials with nonfluent apparent motion trials and vice versa, after collapsing across body and nonbody stimuli.

To assess the neural correlate of the body-specific temporal bias during ABM perception the following interaction was computed: (body/fluent > body/nonfluent) > (nonbody/fluent > nonbody/nonfluent). This interaction revealed that for body stimuli (compared with nonbody stimuli) fluent ABM led to greater activity than nonfluent ABM in a motor cluster comprising the medial part of the primary motor cortex (M1) and the posterior supplementary motor area (SMA). Note that the interaction term controls for lower-level visual processing effects by the (blurred) nonbody control stimuli (see Fig. 1C, Table 1 and Supplementary Fig. 2). The reverse interaction contrast did not reveal any significant activation (see Table 1). Notably, the simple effect of body/fluent > body/nonfluent revealed a significant cluster

**Table 2** SVC analysis body versus nonbody contrast

| Body > Nonbody | Hemisphere | Cluster size (voxels) | Max *T*-value | MNI coordinates | | |
|---|---|---|---|---|---|---|
| | | | | x | y | z |
| SVCs (8 mm sphere, all $P < 0.01$, FWE corrected) | | | | | | |
| Middle temporal gyrus (EBA) | R | 235 | 7.99 | 50 | −68 | 0 |
| | L | 147 | 6.18 | −52 | −74 | 2 |
| Fusiform gyrus (FBA) | R | 94 | 4.71 | 46 | −48 | −22 |
| | L | 131 | 5.54 | −42 | −44 | −26 |
| pSTS | R | 252 | 6.18 | 52 | −54 | 4 |
| | L | 59 | 4.18 | −52 | −58 | 4 |
| Parahippocampal place area (PPA) | R | No suprathreshold clusters | | | | |
| | L | No suprathreshold clusters | | | | |

Small volume correction centered at average coordinates for EBA, FBA, and pSTS based on Grosbras et al. (2012): right EBA [50 −68 −2] and left EBA [−44 −74 2]; right pSTS [54 −54 10] and left pSTS [−52 −50 4]; and right FBA [42 −54 −20] and left FBA [−40 −48 −20]. Coordinates for PPA were based on Peelen and Downing (2005) converted from Talairach to MNI space using mapping from Lacadie et al. (2008); right PPA [28 −39 −16] and left PPA [−25 −44 −16].

PPI, psychophysiological interaction; SVC, small volume correction; EBA, extra-striate body area; FBA, fusiform body area; pSTS, posterior superior temporal sulcus; PPA, parahippocampal place area; L, left, R, right

**Table 3** Results of the PPI analysis for body stimuli with seed region M1/SMA

| | Hemisphere | Cluster size (voxels) | Max *T*-value | $p_{FWE}$-value | MNI coordinates | | |
|---|---|---|---|---|---|---|---|
| | | | | | x | y | z |
| Whole-brain analysis ($P = 0.005$ uncorrected, $P < 0.05$ at cluster level) | | | | | | | |
| Left parietal cortex | L | 785 | 4.34 | | −30 | −50 | 40 |
| SVCs (8 mm sphere) | | | | | | | |
| Middle temporal gyrus (EBA) | R | 15 | 3.10 | 0.051 | 50 | −66 | 4 |
| | **L** | **42** | **3.16** | **0.046** | **−44** | **−80** | **0** |
| Fusiform gyrus (FBA) | **R** | **137** | **4.02** | **0.008** | **40** | **−58** | **20** |
| | L | 4 | 3.06 | 0.054 | −40 | −48 | 28 |
| pSTS | R | No suprathreshold clusters | | | | | |
| | **L** | **12** | **3.25** | **0.039** | **−52** | **−50** | **12** |
| Parahippocampal place area (PPA) | R | No suprathreshold clusters | | | | | |
| | L | No suprathreshold clusters | | | | | |

The cluster in right FBA clearly survived small volume correction ($p_{FWE/SVC} = 0.008$). However, the clusters in left EBA ($p_{FWE/SVC} = 0.046$) and left pSTS ($p_{FWE/SVC} = 0.039$) just survived the predefined threshold of $p_{FWE/SVC} < 0.05$, while the clusters in right EBA ($p_{FWE/SVC} = 0.051$) and left FBA ($p_{FWE/SVC} = 0.054$) just failed to reach this significance level. For right pSTS, no supra-threshold clusters were observed. Note that no supra-threshold clusters were found for PPA bilaterally. Small volume correction with an 8 mm sphere centered at average coordinates for EBA, FBA, and pSTS based on Grosbras et al. (2012): right EBA [50 −68 −2] and left EBA [−44 −74 2], right pSTS [54 −54 10] and left pSTS [−52 −50 4] and right FBA [42 −54 −20] and left FBA [−40 −48 −20]. Coordinates for PPA were based on Peelen and Downing (2005) converted from Talairach to MNI space using mapping from Lacadie et al. (2008); right PPA [28 −39 −16] and left PPA [−25 −44 −16].
PPI, psychophysiological interaction; SVC, small volume correction; EBA, extra-striate body area; FBA, fusiform body area; pSTS, posterior superior temporal sulcus; PPA, parahippocampal place area; L, left, R, right.

encompassing the primary motor cortices (M1) of both hemispheres (Cluster size 1688 voxels, maximum *T*-value: 5.38, MNI peak coordinates: −6 −32 68; see Supplementary Results and Fig. 2).

To closely inspect the modulation of STS, FBA, and EBA activation across conditions, we performed an ROI analysis. We used average $\beta$ estimates for 8 mm spheres surrounding the peak coordinates from Grosbras et al. 2012 using a 2 (hemisphere) × 2 (stimulus type) × 2 (movement fluency) × 2 (SOA) repeated-measures ANOVA. The findings mirror those from the whole-brain analysis, showing body specificity in all 3 areas that is more pronounced in the right hemisphere, but no significant influence of motion fluency (see Supplemental Results and Fig. 1).

### Psycho-physiological Interaction

To investigate whether the activity in the motor cluster (as revealed by the interaction term) is functionally coupled to brain areas associated with body/movement perception, functional connectivity between this motor cluster and EBA/pSTS/FBA was assessed by computing PPIs. At the whole-brain level, activity in the motor cluster was significantly correlated with left parietal cortex activity (see Table 3). SVCs revealed significant or close to significant increases in functional connectivity between the motor cluster and the middle temporal gyrus (EBA) and the fusiform gyrus (FBA) in both hemispheres, and between the motor cluster and left pSTS. This sequence-specific connectivity increase was particularly striking for right FBA (see Fig. 1E and Table 3). Since the levels of significance ($p_{FWE}$) in EBA and pSTS were ~0.05, we tested the robustness of our findings by increasing the size of the search volume. Using a 12 mm sphere only right FBA ($T = 4.1$, $p_{FWE} = 0.02$, cluster size: 292 voxels, peak MNI coordinates [40 −62 −22]) reached significance, while we observed no significant supra-threshold clusters in EBA and pSTS with this sphere size (12 mm). Note that for both sphere sizes (8 and 12 mm), no significant supra-threshold clusters were found in the PPA. Similarly, running the PPI for nonbody stimuli did not reveal any significant activation clusters, either at the whole-brain level, or after SVC.

Accordingly, the motor activation that underpinned our perceptual task was related to body-specific information processing in right FBA, with less robust evidence for an involvement of EBA and pSTS in ABM perception.

## Discussion

By using an implicit perceptual correlate of ABM, we were able to characterize a brain mechanism that is involved in perceiving movement from purely static displays of the human body. Our research suggests, for the first time, a missing link between the brain areas involved in visual body perception (EBA/FBA and pSTS) and those involved in action control (primary and SMAs). Our findings suggest that reconstructing human movement from static body postures is not a purely visual process (Jellema and Perrett 2003; Barraclough et al. 2006), but additionally involves recurrent activity between traditionally visual areas underlying body perception and motor areas classically associated with control of body movement.

Previous work proposed the concept of "motor resonance" to describe automatic increases in motor excitability during action observation (Fadiga et al. 1995, 2005). Likewise, human fMRI studies showed activations of motor areas when merely observing actions (Stevens et al. 2000; Saygin et al. 2004; Calvo-Merino et al. 2005, 2006; Dayan et al. 2007; Gazzola and Keysers 2009; Kilner and Lemon 2013; Gardner et al. 2015) and for biological motion that refers to motor codes for one's own actions (Astafiev et al. 2004; Casile and Giese 2006; Cross et al. 2006; Orlov et al. 2010; Kirsch and Cross 2015). However, our study provides the first clear demonstration that classical motor areas of the cerebral cortex are involved in the perception of human movement, even when the motion percept is constructed from purely static stimuli, and even when ABM is irrelevant to the task (Orgs et al. 2011a, 2011b, 2013b).

Interestingly, and in line with the PET study by Stevens et al. (2000) this activation was primarily located in the medial primary and supplementary motor areas rather than in the more ventral premotor areas classically associated with the MNS. A number of studies have reported "mirror-like" activity in M1, at both

single-neuron (Tkach et al. 2007; Vigneswaran et al. 2013) and population levels (Dushanova and Donoghue 2010). Neurons with mirroring properties have also been found in the human SMA (Mukamel et al. 2010).

Additionally, the medial location of the motor activity found in the current study could reflect a somatotopic response to whole-body ABM: Our stimuli mainly involved movements of the legs and torso, which are somatotopically represented rather medially in M1, and did not involve hand, digit, or face movements, which are represented in lateral M1. This interpretation is supported by the localization of our activations in the STS. Specifically, we found increased activation in posterior rather than middle parts, consistent with previous reports that the posterior STS preferentially responds to whole-body motion, while the middle STS preferentially responds to face and hand motion (Puce and Perrett 2003; Grosbras et al. 2012).

Conceivably, activity in (pre-)SMA may also be related to duration estimation (Macar et al. 2006; Coull et al. 2008). However, SMA activations associated with time perception are generally found more anterior to the motor cluster in our study, and usually do not extend into M1. Importantly, our study distinguishes brain areas that process objective duration differences (SOA) from brain areas that are associated with duration biases caused by the perception of fluent ABM. Activity in SMA and M1 was associated with the bias in subjective duration induced by viewing fluent ABM sequences of body stimuli. Conversely, activity in SMA and M1 was not associated with objective differences in stimulus timing (i.e., the main effect of long vs. short SOAs), although this stimulus manipulation produced greater activity in early visual areas (Muckli et al. 2002; Sterzer et al. 2006) and in the inferior and middle frontal gyri (see Table 1). Accordingly, motor involvement during fluent ABM perception is unlikely to reflect bottom-up features of the visual stimulation. Instead motor involvement reflected perceptual changes in the subjective duration of a single stimulus sequence, as a result of its fluent or nonfluent motoric organization. This suggests that SMA and M1 are involved in the brain processes that transform sequences of static body postures into dynamic percepts of movement speed and fluency (Orgs et al. 2011a, 2011b, 2013a).

Our PPI analysis implies that the brain mechanisms underlying ABM perception involve increased functional connectivity between M1/SMA and left parietal cortex as well as between M1/SMA and right FBA. Less robust increases in functional connectivity were also found in left pSTS and bilaterally in EBA. The same PPI conducted for nonbody stimuli produced no significant increases in functional connectivity between these areas. Accordingly, our findings suggest at least an indirect role of perceptual body areas and more specifically FBA, in ABM perception. These visual areas might either provide input to motor areas or receive top-down input from motor areas, forming a recurrent visual-motor network for reconstructing dynamic movement from static inputs. PPI does not allow us to distinguish between these 2 possible directions of information flow within the network. Moreover, future studies might combine our ABM paradigm with a functional localizer approach, to specifically identify the respective contribution of EBA, FBA, and pSTS to ABM perception.

Our findings clearly suggest a distinction between body representations in FBA and EBA: Functional connectivity in our study was more consistent between FBA and motor areas than between EBA and motor areas. This pattern of results is consistent with the proposed hierarchical organization of these 2 areas in body representation (Ewbank et al. 2011). Compared with EBA, visual representations in FBA are supposedly configural (whole-body) and more closely linked to the subjective percept (Taylor and Downing 2011; Bernstein et al. 2014). Our data are consistent with this hypothesis, and moreover suggest that the distinctive FBA contribution is linked to the perception of dynamic movement.

Traditional paradigms to study visual perception of bodies (using static presentation of a single-body posture or body part) or perception of biological motion (using point light walkers) suggested that the visual body areas EBA and FBA primarily process body shape, whereas STS primarily processes movement kinematics (Downing and Peelen 2011; Vangeneugden et al. 2014). Downing et al. (2006) showed larger responses to incoherently ordered posture sequences as compared with coherent sequences in EBA. Passive observation of correctly ordered sequences was associated with BOLD signal increases in supra-marginal and inferior frontal gyri, the dorsal precuneus, the postcentral junction, and the ventral OTC, but not the primary motor cortex. Our study differs in 3 key respects. Firstly, Downing et al. (2006) presented image sequences at a relatively slow rate (fixed SOA of 633 ms, no blank interval), with the deliberate intention of avoiding perceived motion. In contrast, presentation rates in our study were shorter and consistent with SOAs that typically induce ABM (Shiffrar and Freyd 1990, 1993; Orgs et al. 2011a, 2011b). Secondly, participants in the Downing et al. (2006) study were instructed to attend to the body-posture sequences. In contrast, our study used time perception as an indirect behavioral index of the vividness of apparent motion perception. Thirdly, some actions in their study implied interactions with objects (e. g. kicking, combing one's hair). Accordingly, scrambling these actions does not only disrupt implied movement fluency, but also eliminates the correct order of a meaningful action sequence. It is thus not clear whether increased activity for incoherent sequences is related to a lack of perceptual movement fluency, or rather reflects a prediction error arising from disrupting the normal order of goal-directed action sequences (Grafton and Hamilton 2007). In contrast, all body-posture sequences in our study were derived from abstract dance movements that do not have a familiar or logical order. Therefore, all combinations of these body postures produced equally plausible movement sequences, without any specific meaning.

Importantly, the ABM percept was irrelevant to our subjects' task: they were instructed to judge the duration of the surrounding white rectangle, ignoring the apparent motion stimuli. This instruction might potentially reduce the strength of activations in our study. However, any recruitment of motor areas would then occur spontaneously, without any requirement to attend to or interpret movement. Participants in a previous imaging study using PET (Stevens et al. 2000) explicitly judged movement feasibility. The activations in their study might therefore result from explicit movement imagery or motor simulation, rather than from automatic reconstruction of a movement percept. In contrast, our study provides an implicit, perceptual measure of a "motor way of seeing" (Calvo-Merino et al. 2005, 2006). Further, fluent and nonfluent ABM sequences in our study were created from identical static body postures, and nonbody stimuli were matched for lower-level features; our findings are thus not easily explained by differences in bottom-up visual information.

Our behavioral findings suggest a residual temporal bias for the nonbody stimuli. Moreover, motor cortical activation was reduced, but not entirely absent, when viewing our abstract control stimuli (Fig. 1D). This residual motor activation may reflect the seemingly automatic attribution of intentions and even feelings to the motion of abstract shapes such a triangles or circles (e.g., Heider and Simmel 1944; Bloom and Vrees 1999). Neural mechanisms of extracting intentions from observed movement can be triggered by simple geometric shapes by means of associative

learning (Press et al. 2012). Using pixelated versions as controls for our body stimuli in our study may have underestimated body-specific temporal biases and related motor resonance to ABM.

To summarize, we show that motor areas are involved in the perception of ABM from static sequences, in the absence of any actual movement. BOLD responses in a motor cluster reflected a subjective bias in time perception, specific to ABM of fluent movements. This surprising input-driven activation of classically motor output areas was associated with the generation of a dynamic percept of movement from static visual stimuli. Our study shows that brain areas traditionally associated with voluntary motor control also contribute to the visual perception of human movement. This finding provides a novel complement to studies that attribute motor functions to traditionally visual areas (Astafiev et al. 2004; Orlov et al. 2010; Bracci and Peelen 2013). Conversely, our study implies a perceptual function of motor areas. This suggests a neuroanatomical revision of the traditional visual-to-motor feedforward architectures that have been inherited from the visuo-motor skills tradition (Goodale and Milner 1992; Jeannerod 2001). In this sense, the human brain does not simply encode the actions of others, but constructs these actions, using the cortical motor apparatus. As such, we show that the "motor way of seeing" is engaged spontaneously by appropriate body stimuli (Calvo-Merino et al. 2005, 2006; Orgs et al. 2008). Our results are consistent with the recruitment of a basic system of motor resonance in the human brain for essentially perceptual purposes (Fadiga et al. 1995, 2005).

## Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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