The extrastriate cortex distinguishes between the consequences of one's own and others' behavior

Nicole David,[a,]* Michael X Cohen,[b,c] Albert Newen,[d] Bettina H. Bewernick,[a] N. Jon Shah,[e,f] Gereon R. Fink,[e,f,g] and Kai Vogeley[a,f]

[a]*Department of Psychiatry and Psychotherapy, University of Cologne, Kerpener Str. 62, 50924 Cologne, Germany*
[b]*Department of Psychology, University of California Davis, USA*
[c]*Department of Epileptology, University of Bonn, Germany*
[d]*Department of Philosophy, University of Bochum, Germany*
[e]*Institute of Neuroscience and Biophysics, Department of Medicine, Research Center Juelich, Germany*
[f]*Brain Imaging Center West, Research Center Juelich, Germany*
[g]*Department of Neurology, University of Cologne, Germany*

The extrastriate body area (EBA) is traditionally considered a category-selective region for the visual processing of static images of the human body. Recent evidence challenges this view by showing motor-related modulations of EBA activity during self-generated movements. Here, we used functional MRI to investigate whether the EBA distinguishes self- from other-generated movements, a prerequisite for the sense of agency. Subjects performed joystick movements while the visual feedback was manipulated on half of the trials. The EBA was more active when the visual feedback was incongruent to the subjects' own executed movements. Furthermore, during correct feedback evaluation, the EBA showed enhanced functional connectivity to posterior parietal cortex, which has repeatedly been implicated in the detection of sensorimotor incongruence and the sense of agency. Our results suggest that the EBA represents the human body in a more integrative and dynamic manner, being able to detect an incongruence of internal body or action representations and external visual signals. In this way, the EBA might be able to support the disentangling of one's own behavior from another's.
© 2007 Elsevier Inc. All rights reserved.

Keywords: Extrastriate body area; Extrastriate cortex; Sense of agency; Self–other distinction; Functional connectivity; fMRI

Introduction

The extrastriate body area (EBA), a region in occipital–temporal cortex, has been described as a category-selective region that responds predominantly to static pictures of the human body and not to pictures of other stimulus categories such as objects (e.g., a spoon, a brush, etc.) (Downing et al., 2001, 2006b; Urgesi et al., 2004; Peelen and Downing, 2005; Saxe et al., 2006; Peelen et al., 2006; Spiridon et al., 2006). This domain-specificity hypothesis of EBA function has been recently challenged by a demonstration of increased EBA activity for self-generated pointing movements, independent of the perception of the limb (Astafiev et al., 2004, 2005; cf. Peelen and Dowing, 2005), suggesting that EBA's function is not purely perceptive but extends into the motor domain. Other authors have made similar suggestions for activation in coordinates matching previously published EBA coordinates or for the over-lapping/adjacent motion-specific area hMT+ (Schenk et al., 2000; Oreja-Guevara et al., 2004; Hamilton et al., 2005; Jackson et al., 2006).

The findings of Astafiev et al. (2004, 2005) suggested an encoding of internal, action-related signals such as central motor and proprioceptive feedback signals within the EBA. This opened the possibility that the EBA is also involved in distinguishing whether actions are caused by oneself or by another person. This self–other distinction is a prerequisite for the sense of agency, the ability to recognize oneself as the originator or initiator of one's own behavior (Gallagher, 2000). This internal –and not necessarily conscious– comparison between efferent signals arising from action preparation and reafferent sensory signals arising from action execution and observation or, in other words, the comparison between predicted and actual sensory outcome (Wolpert et al., 1995; Blakemore et al., 1998; Blakemore and Frith, 2003), has been proposed as one important mechanism for the sense of agency. This influential account has triggered a line of experiments that manipulated reafferent sensory, particularly visual, signals to create a mismatch between action intentions, predictions, and actual outcomes.

Using functional magnetic resonance imaging (fMRI), we sought to evaluate a contribution of the EBA to the sense of agency by detecting mismatches between internal and external action- or feedback-related signals. We used a task in which subjects performed simple joystick movements while the visual feedback of their movements was manipulated in half of the trials. On such trials, subjects were told they would see the visual feedback to movements carried out by the experimenter. Our task was based on a previously published experimental manipulation (e.g., Nielsen, 1963; Farrer and Frith, 2002; Farrer et al., 2003; Fourneret and Jeannerod, 1998; Franck et al., 2001; Knoblich and Kircher, 2004; MacDonald and Paus, 2003), which creates a mismatch between the executed movement and its observed, visual outcome. We used an independent functional localizer to identify the EBA individually for each subject, and then examined activity in the EBA during the joystick task. Importantly, there were no images of body parts or other complex visual stimuli during the task, so any differences in activity in EBA could not be attributed to visual perception of the human body or other complex visual images.

It is important to note a discrepancy with recent research on the EBA: some propose it is most active during self-generated movements in the absence of visual feedback (Astafiev et al., 2004, 2005; Jeannerod, 2004), whereas other findings suggest that the EBA is most active during viewing of other people's bodies (Chan et al., 2004; Saxe et al., 2006). We suggest that the EBA detects violations of internal body or action representations and external visual signals (in accordance with Avikainen et al., 2003; Chan et al., 2004; Saxe et al., 2006), a mechanism that the sense of agency may rely on when actions are identified as self-generated or generated by other agents. Such a capacity would go beyond a merely visual and static representation of the human body within the EBA and suggest the need to reconsider the function of the EBA.

Materials and methods

Subjects

Nineteen healthy male volunteers with no significant psychiatric or neurological history were studied. Data from one subject were excluded because of poor task performance, from two subjects because of head movement, and from two subjects because of image artifacts. Thus, data from the remaining 14 subjects (mean age 25.6 years; range 19–33 years) are reported. All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained before participation. The study was approved by the local ethics committee.

Task and experimental design

The task was programmed and presented using the Presentation software (Neurobehavioral Systems, Albany, CA, USA). Subjects performed simple right-handed joystick movements towards one of two objects (an asterisk or a triangle) located on either the upper left or upper right side of the screen. On each trial, a visual cue (e.g., an asterisk) located at the upper center indicated the target object towards which subjects should move a cursor (Fig. 1). Subjects were told that on half of the trials they would not see their own movements, but instead would see cursor movements driven by the experimenter, who performed the task simultaneously outside the scanner. This was a *cover story* in order to elicit activation in neural circuits involved in the perception of other humans (or other humans' actions), in contrast to, for example, a non-human agent such as a computer (Rilling et al., 2004). In fact, though, the experimenter did not influence the task; instead, incongruent feedback trials were recorded self-generated movements from
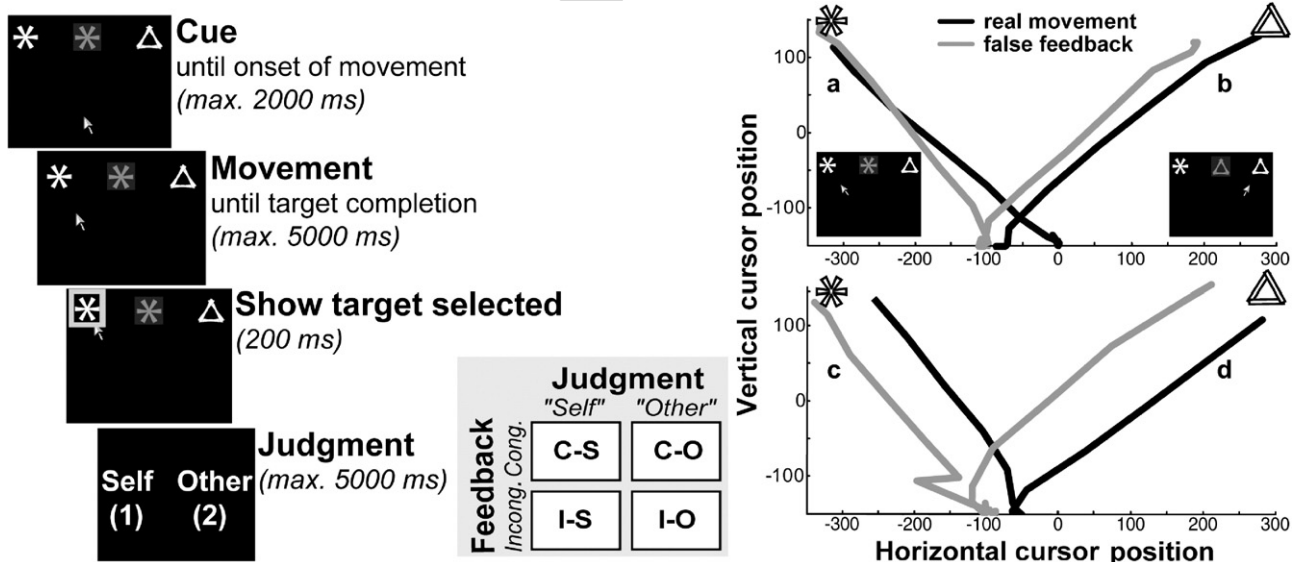
Fig. 1. Task design and movement trajectories. Left panel depicts the task and time course of a trial (time flows from top to bottom). Subjects saw a cue (centered grey symbol) and moved a joystick towards the corresponding target to the left or right. The target was highlighted as soon as the cursor reached the target. After this, subjects decided whether the visual feedback was self-generated or not. There were four possible conditions (middle bottom panel): congruent feedback trial judged as self-generated (C-S), congruent feedback trial judged as other-generated (C-O), incongruent feedback trial judged as self-generated (I-S), incongruent feedback trial judged as other-generated (I-O). Right panel shows, for one subject, examples of small (top row) and large (bottom row) spatial deviations between congruent movement (black line) and incongruent feedback (gray line), at which the incongruent feedback was incorrectly judged as "self" (I-S; A and C) and correctly perceived as "other" (I-O; B and D). x- and y-axes represent horizontal and vertical cursor positions on the screen.

randomly selected previous trials the subject had already performed (see next paragraph). This avoided systematic differences between feedback conditions, because subjects served as their own controls. Immediately after the target had been reached with the cursor (i.e., the end of movement), the display showed the words "self" and "other," prompting subjects to indicate whether the movement they saw was driven by themselves or by the "experimenter" (Fig. 1). The subsequent judgment of a movement/feedback gave rise to a quasi two-by-two design (*quasi* because the factors cannot be considered truly orthogonal) with the factors Feedback Manipulation (subjects being the author of the movement, "congruent feedback", or not, "incongruent feedback") and Judgment (feedback judged as "self-generated" or "other-generated"; Fig. 1).

Subjects were instructed to react quickly, avoid jerky movements, and always perform a movement even if they thought that the experimenter controlled the movement. The incongruent visual feedback could differ in onset, velocity, and kinematics, as compared to the actually executed movement, as well as by path deviations. Path deviations were limited in the sense that the incongruent visual feedback always went to the target that was indicated by the cue, i.e., in the same direction as the subjects' intended movement. Note that we wanted the possibility to statistically examine correct vs. incorrect attributions, we thus designed the task to be difficult. In order to play back pre-recorded movement sequences (i.e., incongruent condition), the x- and y-coordinates of the subjects' actual movements during each trial were recorded and written to a text file stored on the computer, with a sampling rate of approximately 60 Hz. During incongruent trials, the program selected one of these previously recorded movement sequences at random, and adjusted the position of the cursor on the screen at each monitor refresh, such that the experiments displayed the x- and y-coordinates of a previous trial, and not the subjects' actual current movement. This sequence was automatically initiated once the subject moved the joystick from the starting point. The speed with which the program displayed the mouse position was overall similar to the speed with which subjects actually moved.

Target locations were at $x = -300$ and $y = 150$ pixels from the center of the screen (1024×768 resolution) for the asterisk and $x = 300$ and $y = 150$ for the triangle (the center of the screen was at x, $y = 0$). We defined target zones ($x = \pm 260$ and $y = 100$): if the cursor hit the edge of these zones the target would get selected and highlighted. For the post-trial rating, subjects pressed a corresponding key on an MRI-compatible hand-held response device using the left hand (Lumitouch, Lightwave Medical Industries, CST Coldswitch Technologies, Richmond, CA, USA). Subjects used either the left middle or index finger (middle finger = self-generated; index finger = other-generated).

There were 136 trials for each feedback condition (68 movement trials to the left, 68 to the right target). The experiment was scanned in four sessions, which differed in the sequence of left/right target trials and their respective feedback as congruent or incongruent. Left- and right-directed movements were counterbalanced in order to avoid any biased influence of the visual hemifield on brain activation. In addition, the intertrial interval was differently jittered (6–12 s) and randomized within and across the four sessions. The order of scanning sessions was randomized across subjects. Before scanning, subjects practiced the task outside and inside the scanner to get used to the task and to ensure they were comfortable with the bimanual responses and the MRI-compatible joystick. This joystick did not have a metal centering spring, allowing the joystick to jump back to point zero. Therefore, subjects were instructed to pull the joystick towards themselves after each trial (middle front position). This procedure was practiced and monitored before scanning in order to guarantee a similar starting point for each trial within and between subjects. There were no systematic differences between congruent and incongruent feedback with respect to starting positions as randomly selected real movements served for later incongruent feedback trials. Inside the scanner, subjects looked through a mirror mounted on the head coil to see a screen, on which stimuli were projected. After scanning, subjects did short informal written debriefings, which asked (i) how incongruent feedback was recognized trials, (ii) how fast it was recognized, (iii) how difficult it was to make agency judgments, and (iv) how secure subjects felt about those judgments.

Statistical analyses of behavioral data

All statistical analyses were performed using the software SPSS for Windows (version 12.0) and were tested two-tailed at a significance level of $P < .05$. Non-parametric statistics (Friedman and Wilcoxon Signed Ranks test) were performed, because the behavioral data failed to meet normality and equality of variance assumptions, with one exception: to test for a possible systematic pattern of event distribution across scan sessions, a four-by-four repeated measures ANOVA was used.

fMRI image acquisition, preprocessing, and analyses

Functional and structural MRI was performed on a Siemens 1.5 T MRI whole body scanner (SIEMENS Sonata, Erlangen, Germany) using a standard head coil and a custom-built head holder to minimize head movements. Functional images were obtained using a single-shot gradient echo, echoplanar imaging (EPI) sequence (TR: 2000 ms, TE: 60 ms, 90° flip angle, FOV: 200 mm, matrix: 64×64, voxel size: $3.1 \times 3.1 \times 4$ mm, 2.5 mm gap). EPI volumes for the main experiment contained 21 axial slices and 245 scans (4 runs, each ~ 8 min) and 20 axial slices and 170 scans (2 runs, each ~ 6 min) for the EBA localizer. Both experiments were obtained in the same fMRI session. To aid in localization of activation, a high-resolution T1-weighted magnetization-prepared rapid gradient-echo imaging (MP-RAGE) 3D sequence was also acquired from each subject (TR: 2200 ms, TE: 3.93 ms, 15° flip angle, FOV: 256 mm, matrix: 256×256, voxel size: $1 \times 1 \times 1$ mm).

Functional images were preprocessed and statistically analyzed using Statistical Parametric Mapping (SPM2, Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB 6.5 (Mathworks Inc., Sherborn, MA, USA). The first three repetitions of each EPI series were discarded before image analyses to allow for T1 saturation effects. Images were reoriented (along the AC-PC line) and eyes were masked to minimize artifacts. Images were then corrected for head movement (realigned and unwarped), slice timing corrected (main experiment only), co-registered, normalized to stereotactic space, re-sampled to a voxel size of $2 \times 2 \times 2$, and spatially smoothed with a 10-mm Gaussian kernel. Hemodynamic responses were modeled with a canonical hemodynamic response function and, for the main experiment, with its first-order temporal derivative.

Statistical analyses were performed on single-subject and group data using the modified general linear model in SPM2. Subject-specific, low-frequency drifts in signal changes were removed by a high pass filter (48 s for the main experiment and 128 s for the EBA localizer experiment) and temporal autocorrelations between

scans were estimated using a first-order autoregressive model. For each subject and each condition, a comparison of interest was implemented as an individual contrast image. For group comparisons, these contrast images were used in a second-level analysis (one-sample *t* tests), treating subjects as a random variable. Trials were classified according to five event-types: (1) congruent feedback correctly judged as self-generated (C-S), (2) congruent feedback incorrectly judged as other-generated (C-O), (3) incongruent feedback incorrectly judged as self-generated (I-S), (4) incongruent feedback correctly judged as other-generated (I-O), and (5) omissions (i.e., trials when no judgment was made). Subjects showed no or only a few omissions, thus, these were not analyzed further.

For the functional connectivity analysis, we used psychophysiologic interaction (PPI) method (Friston et al., 1997), using as a seed regions a 10 mm sphere around the individual EBA peak. For each subject, a psychophysiological interaction was calculated by multiplying this time course with the psychological variable of interest (i.e., the contrast I-O vs. C-S and vice versa). Individual parameter estimates of the interaction term (PPI images) were then entered into a random-effects group analysis and thresholded with an uncorrected height threshold of *P* < .001 and an extent threshold of *k* = 3 contiguous voxels. Resulting activation peaks (reported in MNI coordinates) were superimposed on a normalized high-resolution MP-RAGE (averaged across subjects) and anatomically localized using the Automated Anatomical Labeling map (AAL map) (Tzourio-Mazoyer et al., 2002) as implemented in MRIcro (www.mricro.com) in addition to an atlas of the human brain (Duvernoy, 1999). Brodmann areas (BAs) were derived using the Brodmann area estimates as provided by Talairach and Tournoux (Talairach and Tournoux, 1988) implemented in MRIcro.

EBA localizer and ROI analysis

The EBA localizer protocol was adapted from Downing et al. (2001). Subjects underwent two short sessions (each ~ 6 min). Blocks of images showing body parts (in allocentric perspective) alternated with blocks of images showing object parts. All pictures were gray-scale photographs (Downing et al., 2001). Each session comprised 16 experimental blocks (each 16 s) with 20 pictures each. Every fourth block a baseline-block (fixation) was shown, also for 16 s. Each pictured appeared for 300 ms followed by a 500 ms interstimulus interval. Subjects performed a 1-back repetition detection task during the localizer experiment in order to sustain attention: they had to detect whenever a stimulus appeared twice successively (twice per block).

EBA region-of-interest (ROI) analyses were performed on a subject-by-subject basis. For each subject, the EBA was defined as the set of all contiguous voxels that were significantly more active for viewing body vs. object parts at an uncorrected height threshold of *P* < .0001 within 10 mm radius around the maximum peak for the right and left hemisphere (this procedure and threshold was adopted in accordance with Peelen and Downing, 2005) using SPM2 and Marsbar (http://marsbar.sourceforge.net/). Two subjects' right hemisphere EBA and three subjects' left EBA maximum peak coordinates were not in total concordance with previously published EBA coordinates and also did not seem appropriate on an anatomical overlay. Thus, for those subjects more adequate sub-peaks (as listed by SPM2) were chosen as the center of the ROIs. EBA-ROIs (likewise ROIs for posterior parietal cortex, PPC) were used to extract parameter estimates for effects of

interest during the agency task. Our primary interest was not activation in EBA compared to baseline but rather relative differences between conditions. The parameter estimates were z-transformed for ease in interpretability and cross-subject comparison, and were subsequently entered into a two-way repeated-measures ANOVA, with the factors Feedback Manipulation (congruent vs. incongruent) and Judgment (self vs. other) using ezANOVA (www.sph.sc.edu/comd/rorden/ezanova/home.html). The significance level for this ANOVA was set at *P* < .05. An additional post hoc ROI analysis was carried out by creating a spherical ROI image file with Marsbar (http://marsbar.sourceforge.net/), which was then used as a search volume for the spmT map, using the WKU PickAtlas (Maldjian et al., 2003) as implemented in the SPM2 toolbox (see http://www.fmri.wfubmc.edu).

Results

Behavioral results

Forty-six ± 1% of all trials were congruent feedback correctly judged as self-generated ("congruent-self"; C-S); 5 ± 1% of trials were congruent feedback incorrectly judged as other- (i.e., experimenter) generated ("congruent-other"; C-O); 24 ± 3% of trials were incongruent feedback incorrectly judged as self-generated ("incongruent-self"; I-S); and 26 ± 3% of trials were incongruent feedback correctly judged as other-generated ("incongruent-other"; I-O; Fig. 2). The conditions differed significantly with respect to the number of trials they contained (Wilcoxon test: all *Z* < −3.93, all asympt. *P* = .001), except for I-S and I-O (*P* = .594). There were no changes in performance across the four scanning sessions (ANOVA; *P* = .570). Reaction times (RTs) to judgments (defined as the time delay between the display prompting subjects to make a 'self-or-other' judgment and the button press) ranged from 458 ± 36 ms (C-S) over 505 ± 48 ms (I-S) and 575 ± 39 ms (I-O) to 699 ± 81 ms (C-O) and were significantly different across conditions (Wilcoxon test: all asympt. *P* < .03), except RTs for C-S and I-S, which did not differ significantly from each other (*P* = .124; Fig. 2). Thus, subjects were faster to judge that the movement was self-generated. Motion onset times (when subjects initiated the joystick movements) ranged from 797 ± 33 ms (I-O) to 855 ± 57 ms (C-O) and did not differ significantly between conditions (*P* = .277). In informal post-experiment debriefings, subjects reported to have identified incongruent feedback by temporal (i.e., speed and the onset of the incongruent feedback movement) and spatial deviations. Fig. 1 (right panel) demonstrates, for one subject, examples for small (Figs. 1A, B) and large (Figs. 1C, D) spatial deviations, at which the incongruent feedback was incorrectly judged as "self" (I-S) and correctly perceived as "other" (I-O).

EBA ROI analyses: EBA is more active during incongruent than congruent feedback

We used a localizer experiment that was independent of the main experiment to identify subject-specific, functionally defined EBAs (Supplementary Fig. 1) (Downing et al., 2001, 2006b; Peelen and Downing, 2005; Saxe et al., 2006; Peelen et al., 2006; Spiridon et al., 2006). Statistically significant right hemisphere EBAs were obtained in 13 out of 14 subjects (mean peak coordinates ± standard deviation: 52 ± 3, −70 ± 6, 5 ± 6), whereas left EBAs were identified in 11 of 14 subjects (mean ± standard deviation: −49 ± 5, −76 ± 8, 10 ± 5; for a list of individual
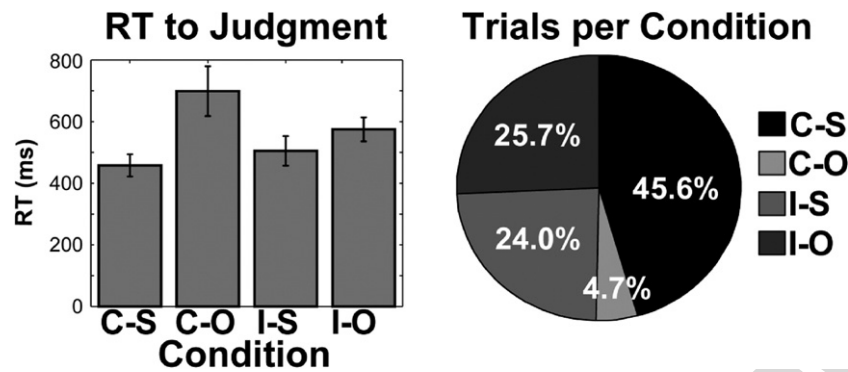
RT to Judgment

Trials per Condition

Fig. 2. Displayed are reaction times (RT) to judgment and the percentage of trials per condition. RTs differed significantly between conditions except for C-S and I-S (significant effect of "Judgment"). The percentage of trials also differed significantly between conditions except for I-S and I-O (significant effect of "Feedback Manipulation").

coordinates see Supplementary Table 1). We then used these individually derived ROIs to examine the EBA's response during the main task.

Activity in the right EBA was significantly greater during incongruent in comparison to congruent feedback trials, i.e., when there was a mismatch between the executed movement and visual feedback ($F_{1,12}=5.5$, $P=.037$) (Fig. 3). Importantly, subjects neither observed their own limbs nor images of body parts or any other complex objects. How subjects judged the feedback manipulation (i.e., as self-generated or not) did not significantly influence activity in the EBA ($P=.750$), nor was there an interaction between feedback judgment and feedback manipulation ($P=.600$). A similar pattern of results was observed in left EBA, but did not reach significance ($P=.160$ for the main effect of feedback). Note that fewer subjects were included in this analysis because not every subject had an identifiable left EBA.

Whole-brain group-analyses

Main effect of feedback

We also conducted less spatially restrictive but more statistically stringent whole brain analyses to examine other regions in which our feedback manipulation modulated activity irrespective of judgment. We found regions implicated in action representation and execution (e.g., Buccino et al., 2004; Chaminade and Decety, 2002; Farrer and Frith, 2002; Jackson and Decety, 2004; Ramnani and Miall, 2004) such as bilateral middle frontal gyri, left superior parietal (precuneus and postcentral gyrus), bilateral inferior parietal lobule (supramarginal gyrus), the medial aspect of the superior frontal gyrus bilaterally (supplementary motor area), left precentral, and right middle temporal gyrus during incongruent vs. congruent feedback trials (I-S and I-O vs. C-S and C-O; Fig. 4; Table 1).

This contrast also revealed one peak in left occipital–temporal cortex (x, y, $z=-44$, -66, 10; $Z=3.19$; $P=.001$). However, precise localization of EBA on the group level is difficult because of inter-subject functional–anatomical variability (Peelen and Downing, 2005; cf. Spiridon et al., 2006). There were no significantly activated clusters in right occipital–temporal cortex (in contrast to the results of the more sensitive ROI analysis). A recent study that investigated action-specific effects within the EBA also reported contrasting results from whole-brain and ROI analysis (Kable and Chatterjee, 2006). In a post hoc ROI analysis, a restricted search volume centered on the averaged
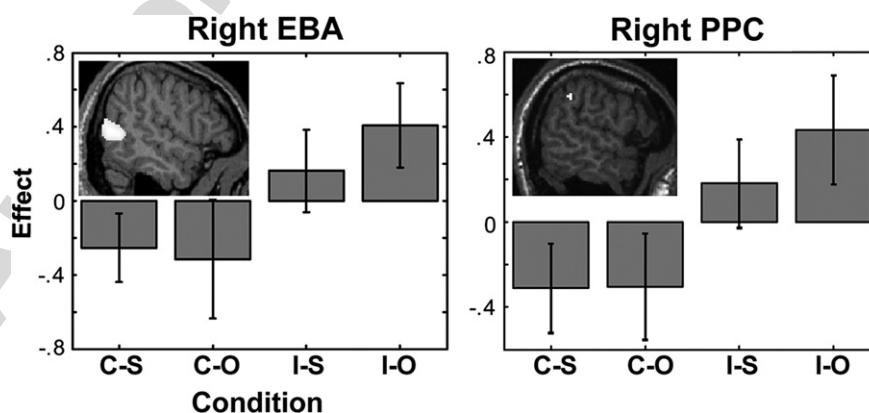
Right EBA

Right PPC

Fig. 3. Activity within the EBA during the experimental task. Mean z-transformed parameter estimates taken from individually localized right EBAs (left panel) and a cluster in right PPC identified in the whole brain analysis (x, y, $z=60$, -42, 38; BA 40; right panel), showing similar response patterns for the EBA and PPC being more activated during incongruent feedback conditions (I-S and I-O) than congruent feedback conditions (C-S and C-O). For illustration purposes, we also displayed a single subject's right EBA and the activation cluster in PPC. Error bars reflect the standard error of the mean across subjects.

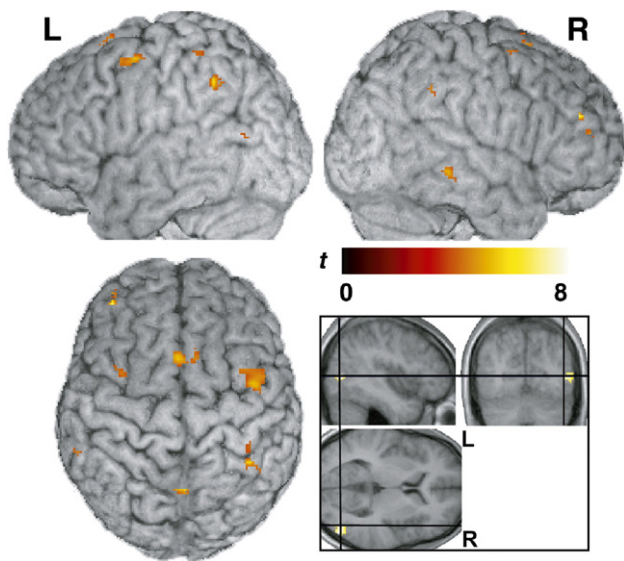Fig. 4. Results of the whole brain analyses. The statistical group activation map for the contrast incongruent (I-S and I-O) greater than congruent (C-S and C-O) feedback was overlaid on a single subject's rendered brain and shows activation of bilateral middle frontal gyri, left superior parietal and bilateral inferior parietal lobule, the medial aspect of the superior frontal gyrus bilaterally, left precentral and right middle temporal gyrus. The smaller panel depicts the restricted search volume based on the averaged individual maxima of right EBA to reveal right occipital–temporal activation for the "incongruent vs. congruent feedback" contrast also on the group level (x, y, z=44, −70, 6 and x, y, z=52, −74, 6).

individual maxima of right EBA (10-mm sphere at x, y, z=52, −71, 5) revealed right occipital–temporal activation for the incongruent vs. congruent feedback (but not the opposite) contrast also on the group level (with two peaks: x, y, z=44, −70, 6; Z=2.24; uncorr. P=.013 and x, y, z=52, −74, 6; Z=2.18; uncorr. P=.015; Fig. 4 smaller panel). Because the location of the EBA may vary across individuals, it may also not be a spatially contiguous region in spatially normalized, group-averaged maps, rendering group-averaged activations in the "EBA" difficult to identify (see also Kable and Chatterjee, 2006). An ROI analysis allowed us to use a less conservative statistical threshold (because of the increased spatial selectivity).

The posterior parietal cortex (PPC) has been repeatedly implicated in the detection of sensory events incongruent to one's own actions (Blakemore and Sirigu, 2003; Chaminade and Decety, 2002; Farrer and Frith, 2002; Farrer et al., 2003; MacDonald and Paus, 2003; Sirigu et al., 1999; Spence et al., 1997). In consequence, the PPC has been suggested as the most likely candidate to code for agency (Jeannerod, 2004). To compare the response in the EBA to the PPC, we also plotted parameter estimates from a cluster in right PPC, specifically in the supramarginal gyrus of the inferior parietal lobule, that we found for the whole-brain analyses "incongruent vs. congruent feedback" (x, y, z=60, −42, 38; BA 40). This comparison showed that the EBA and this region in the inferior parietal lobule responded similarly to the feedback manipulation (Fig. 3).

There were no supra-threshold clusters for the "congruent vs. incongruent feedback" comparison.

Main effect of judgment

We found a significant main effect of "self" (C-S and I-S) vs. "other" (C-O and I-O) judgments in the left precuneus and cuneus, right inferior temporal (fusiform) gyrus, left inferior occipital (lingual) gyrus, right superior temporal gyrus, right putamen, left

Table 1
Main supra-threshold clusters for main effect of feedback manipulation (incongruent ↔ congruent), main effect of judgment ("self" ↔ "other"), and interaction effects (correct ↔ incorrect)

MNI coordinates (x, y, z)			Cluster size	Z score	Anatomical description	BA
Incongruent (I-S and I-O) vs. congruent feedback (C-S and C-O)						
40	44	22	9	4.37	R. middle frontal	45
−2	−64	48	25	3.99	L. precuneus	7
−40	−48	42	33	3.99	L. inferior parietal (supramarginal)	40
2	12	62	54	3.84	R./L. supplementary motor area [a]	6
−42	−2	56	92	3.81	L. precentral/middle frontal[a]	6
52	−34	−10	26	3.70	R. middle temporal	20
40	50	12	6	3.51	R. middle frontal	46
60	−42	38	7	3.46	R. inferior parietal (supramarginal)	40
34	4	60	11	3.32	R. middle frontal	6
−40	−40	58	7	3.24	L. postcentral	2
−44	−66	10	3	3.19	L. middle temporal	37

Congruent feedback (C-S and C-O) vs. incongruent (I-S and I-O): n.s.

Judgment "self" (C-S and I-S) vs. "other" (C-O and I-O)						
−10	−72	58	108	4.20	L. precuneus	7
26	−40	−20	177	4.12	R. inferior temporal (fusiform)	37
−6	−78	−14	120	4.01	L. inferior occipital (lingual)	18
−12	−98	10	45	3.61	L. cuneus	17/18
60	−14	8	7	4.68	R. superior temporal	
28	−4	10	67	4.58	R. putamen	
−38	−16	8	60	4.54	L. insula/putamen[a]	
8	−12	54	11	4.49	R. supplementary motor area	6
−4	−18	62	46	4.40	L. supplementary motor area	6
12	−36	60	10	4.37	R. para-/postcentral	
62	2	−4	7	4.35	R. superior temporal	21/22
−54	−14	12	17	4.19	L. insula	
−54	−26	56	18	4.16	L. postcentral	1/2
−32	0	−6	7	3.25	L. putamen	
−26	−36	70	13	3.15	L. postcentral	3

Judgment "other" (C-O and I-O) vs. "self" (C-S and I-S): n.s.

Correct (C-S and I-O) vs. incorrect (C-O and I-S)						
−64	−8	16	16	3.59	L. postcentral	43
−36	−28	6	21	3.44	L. insula	
−52	−12	16	4	3.23	L. insula	

Incorrect (C-O and I-S) vs. correct (C-S and I-O): n.s.

Note. Anatomical labels according to Duvernoy's atlas of the human brain and the AAL map. R=right hemisphere; L=left hemisphere; BA=approximate Brodmann area.
[a] Extending activation.

insula, supplementary motor area bilaterally, and left postcentral gyrus (Table 1). Some of these areas, such as the SMA, the putamen, and the insula, have previously been associated with the awareness of specifically self-generated actions, action initiation, and the representation of own action intentions (Farrer and Frith, 2002; Farrer et al., 2003; Haggard and Whitford, 2004; Lau et al., 2004; Leube et al., 2003). The opposite contrast, "other vs. self judgments", did not yield significant activations.

Feedback-by-judgment interactions

There was a significant interaction effect of correctly (C-S and I-O) vs. incorrectly (C-O and I-S) judged trials in the left postcentral gyrus and in the left insula (Table 1). No suprathreshold clusters were detected for the opposite contrast.

Functional connectivity between EBA and PPC during correct detection of incongruent feedback

Similar response patterns in the EBA and a region in PPC, the inferior parietal lobule, suggest that the two are functionally related. To statistically investigate this, we conducted two complementary connectivity analyses. First, we correlated the parameter estimates from right EBA and the inferior parietal region. This analysis revealed that the individually extracted parameter estimates from EBA and inferior parietal cortex were positively correlated during C-S (Pearson $r=.73$, $P=.004$), somewhat correlated during I-O conditions (Pearson $r=.50$; $P=.083$), but were unrelated during C-O (Pearson $r=-.06$; $P=.835$) or I-S (Pearson $r=.24$; $P=.241$). Thus the EBA and inferior parietal cortex co-activated during correct judgments of agency.

Second, we used a psycho-physiological interaction (PPI) analysis (Friston et al., 1997) to examine enhanced functional con-

Table 2
Main supra-threshold clusters for functional connectivity (PPI) analysis

MNI coordinates (x, y, z)			Cluster size	Z score	Anatomical description	BA
I-O vs. C-S						
−28	−8	40	55	3.71	L. middle frontal	~6
14	−40	−22	12	3.49	R. cerebellum	30
36	−34	56	46	3.44	R. postcentral	3
40	−84	−12	8	3.38	R. inferior occipital	19
28	−52	54	5	3.31	R. superior parietal	7
−20	−60	44	5	3.26	L. superior parietal	7
22	−66	10	3	3.11	R. calcarine	17
C-S vs. I-O						
−20	−40	60	5	3.76	L. postcentral	2
28	−10	−14	7	3.43	R. medial temporal/ amygdala/insula [a]	20/34

Note. Anatomical labels according to Duvernoy's atlas of the human brain and AAL Map. R=right hemisphere; L=left hemisphere; BA=approximate Brodmann area.
[a] Extending activation.

nectivity (i.e., correlations in the time courses of the blood-oxygen-level dependent, BOLD, response) between the right EBA seed region and other brain regions for correct feedback judgments. This whole-brain connectivity analysis, for the contrast C-S vs. I-O and vice versa, was motivated by the aforementioned significant correlation of parameter estimates in ROIs within the EBA and PPC during correct feedback evaluations. This second analysis also yielded several regions in PPC showing increased connectivity to the EBA as a seed region: activity in left postcentral and right medial temporal cortices (extending into the insula) was correlated with activity in the EBA during C-S compared to I-O (Fig. 5). During the opposite contrast (I-O vs. C-S), activity in several posterior parietal areas such as right postcentral and bilateral superior parietal cortices (among other brain areas such as left middle frontal and right inferior occipital cortex, as well as the right cerebellum, Table 2) was correlated with EBA activity (Fig. 5).

Discussion

Until recently, the EBA has been considered a selective, category-specific area for the static visual representation of the human body (Downing et al., 2001, 2006b; Peelen and Downing, 2005; Peelen et al., 2006). The finding that movement of one's own limbs, without any vision of the movement or the limb, also modulates activity within the EBA challenged this view suggesting that the EBA is not only responsive to visual signals but also to endogenous signals during motor performance (Astafiev et al., 2004, 2005; cf. Peelen and Downing, 2005).

In Astafiev et al. (2004, 2005), the EBA showed increased activity during execution or preparation of visually-guided limb movements in the total absence of visual consequences. Furthermore, their data suggest an encoding of efferent and/or reafferent proprioceptive signals in the EBA. This finding that the EBA showed such a strong response to internal signals in the absence of visual feedback seemed astonishing in light of the EBA being considered a visual area and that neurons in the close neighborhood of the EBA, in the superior temporal sulcus, have been shown to not fire during execution of an unseen action (compare to Miall,
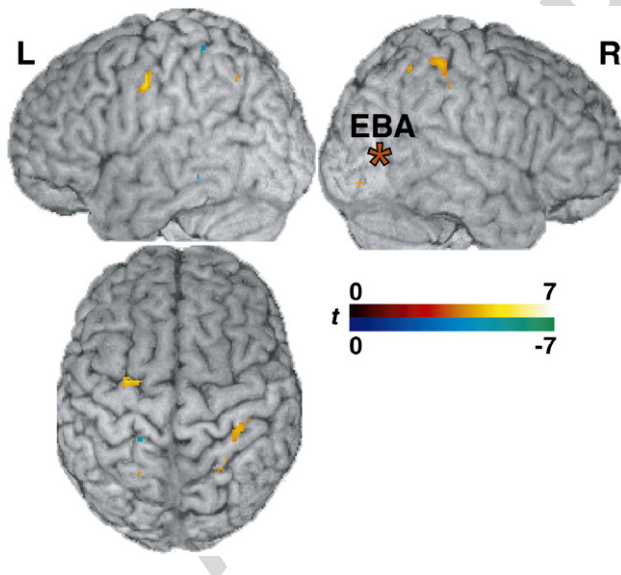

Fig. 5. Results of the functional connectivity analysis. Statistical group activation maps overlaid on a single-subject rendered brain display regions in PPC, specifically right postcentral and bilateral superior parietal regions that showed increased functional connectivity to individually localized right EBA seed regions (approximate location indicated by the asterisk) during the I-O vs. C-S comparison (in orange; note that there was also cerebellar activation which is not visible in this figure). There also was some smaller left postcentral activation during C-S vs. I-O (in blue).

2003). Here we show that the EBA registered reafferent visual signals incongruent to internal – efferent or reafferent proprioceptive – signals. Thus, it seems that the present response in the EBA was most likely driven by differences in visual signals. This is in contrast to Astafiev et al. (2004, 2005) who neither employed a visual feedback nor a mismatch between internal or external signals. Our data, in fact, are more in concordance with findings by Chan et al. (2004) and Saxe et al. (2006) on greater activity in the EBA for images of body parts taken from an allocentric or third-person viewpoint, that is, during a mismatch between internal and external body representations.

Does the EBA play a role in self–other distinctions? The detection of sensory outcome incongruent to executed movements or predicted movement outcome has been linked to the sense of agency for other agents (e.g., Blakemore and Frith, 2003; Farrer and Frith, 2002; Farrer et al., 2003). Again, whereas the data of Astafiev and colleagues would rather suggest an encoding of own actions or body, thus self-agency, our findings rather suggest a response of the EBA to signals not concordant with states of the self, thus other-agency. A recent fMRI study also reports activation in extrastriate cortex, possibly covering the EBA, during visuomotor incongruence (Schnell et al., 2007). In addition, we reported peak activation in group-coordinates matching right EBA more when subjects observed others acting compared to acting themselves (David et al., 2006). The aforementioned experiments by Saxe et al. (2006) and Chan et al. (2004) also suggest greater activation of the EBA for states that reflect others, namely for allocentric more than for egocentric images of body parts as when we are looking at someone else's body (Chan et al., 2004; Saxe et al., 2006; stimuli used in EBA localizers are usually allocentric). Further studies are needed to reconcile our own findings, as well as the findings of Chan et al. (2004) and Saxe et al. (2006), with Astafiev et al. (2004, 2005).

The present findings suggest that the EBA detects violations of internal, possibly multimodal, body or action representations and incoming visual signals (also see Avikainen et al., 2003, on increased extrastriate activation during observation of distorted finger postures), a process that the sense of agency may rely on. A mechanism that might enable the EBA to detect such violations may be cross-modal matching or sensorimotor integration. Indeed, this has been described for other occipital–temporal areas (e.g., the superior temporal sulcus, area hMT+, etc.; Iacoboni et al., 2001; Beauchamp, 2005). Spatial representations or encoding, such as in allocentric coordinates, may represent another mechanism (Chan et al., 2004; Saxe et al., 2006) by which the extrastriate cortex contributes to the sense of agency. In a similar vein, Wegner et al. (2004) have previously claimed that body or environment orientation cues are important for the sense of agency. With respect to the present data, an incongruent visual feedback to the subjects' executed movement may have triggered allocentric representations. Indeed, it has been suggested that others' actions are remapped and represented in allocentric coordinates (Farrer and Frith, 2002; Jeannerod, 1999). This may also answer the question as to why self–other distinction – be it on the level of body perception, body schema or actions – already occurs so early in the visual processing stream. The present empirical evidence supports theoretical claims that agency processing may already occur at early stages of action and perception rather than at higher level cognitive processing (Wegner et al., 2004).

The EBA registered the incongruent feedback but this response was not always associated with correct behavioral evaluations of the incongruent feedback. Thus, activity in the EBA did not perfectly correlate with post-trial (and, presumably, conscious) reports. A similar dissociation between detection or correction of sensorimotor discrepancies and conscious processing of these incongruencies has been previously reported (Slachevsky et al., 2001; Fourneret and Jeannerod, 1998). A neural response towards sensorimotor incongruencies, on which subjects could not explicitly report on, has also been shown for the cerebellum (Blakemore and Sirigu, 2003: "the discrepancy signaled by the cerebellum is not available to awareness."). We seem mostly unaware of the comparison, and the result thereof, of efferent and reafferent signals, or observed and predicted sensory action consequences respectively (Wolpert et al., 1995; Blakemore et al., 1998), especially in the absence of striking incongruencies (Blakemore and Sirigu, 2003; Pacherie, 2001; Slachevsky et al., 2001). Thus, a lack of judgment effect does not exclude a potential contribution of the EBA to agency processing based on the detection of visuomotor incongruencies.

Recent conceptual developments suggest a distinction between two experiential and processing levels: an implicit, *feeling* of agency and explicit, *judgments* of agency (Synofzik et al., in press; also see Wegner et al., 2004). According to Synofzik et al., the implicit level is characterized by automatic, pre-reflective sensorimotor processes whereas the explicit level involves higher-order, reflective, and belief-like processes. Furthermore, the authors are in favor of a two-step model: first, a feeling of agency arises which must then be conceptually processed so that a judgment on or attribution of agency arises. This is in agreement with the idea that agency processing already occurs at early stages of action and perception below the level of higher cognitive processes (Wegner et al., 2004). Applying this idea to our findings, extrastriate activation in response to sensorimotor incongruence may already happen on an early level, whereas awareness or attribution processes occurs elsewhere in the brain. Dehaene et al. (2006) also suggested that preconscious processing is associated with occipital–temporal activation but only spreading of this activation to higher cognitive areas, such as premotor or prefrontal cortices, allows consciousness (e.g., Slachevsky et al., 2001; Ehrsson et al., 2005). The distinction between different experiential or processing levels of agency is interesting but requires further conceptual and direct empirical investigations.

Several regions in the PPC have been implicated in the detection of sensorimotor incongruence, and the representation of other agents and perspectives (e.g., Blakemore and Sirigu, 2003; Chaminade and Decety, 2002; David et al., 2006; Farrer and Frith, 2002; Jeannerod, 2004, MacDonald and Paus, 2003). Right EBA and right inferior parietal lobule (compare to Farrer and Frith, 2002; Farrer et al., 2003) showed a similar response pattern: significantly increased activity during incongruent in comparison to congruent feedback. Similarity suggests that the two areas are functionally related. Anatomical studies in primates indeed show inputs from extrastriate areas to posterior parietal areas associated with sensorimotor integration (Ungerleider and Desimone, 1986; Lewis and Van Essen, 2000; for some discussion of evidence in humans also see Beauchamp, 2005). Importantly, a correlation of the BOLD responses also revealed an increased functional connectivity of PPC and the EBA, with the right postcentral cortex showing increased connectivity to the EBA during correctly identified mismatches of visual feedback to own movements. Interestingly, the cerebellum – also involved in the prediction and monitoring of sensory action outcome (compare to

Blakemore and Sirigu, 2003; Blakemore et al., 2001) – was also correlated with the EBA during correct detections of visuomotor incongruence. The left postcentral gyrus showed increased connectivity to EBA when subjects correctly identified that they drove the visual display themselves. A similar lateralization within the PPC has been previously reported for motor imagery from someone else's perspective (right hemisphere) or one's own perspective (left hemisphere; Ruby and Decety, 2001). We suggest that during correct judgments of visual feedback with respect to executed movements, the EBA and PPC work in conjunction.

Note that when examining the EBA and inferior parietal cortex separately, in the ROI analyses, there were no significant effects of judgment or feedback-by-judgment interactions (but there was an effect of self vs. other judgments from the whole brain analysis for areas in left precuneus and postcentral gyrus). The functional connectivity analysis does not contradict these findings as, first, it is different from main effects analyses in testing for a correlation of the BOLD time courses between brain regions under certain conditions and not for increases in the BOLD response relative to baseline or another condition. Second, a closer visual inspection of the incorrectly in comparison to the correctly judged trials from the ROI analyses shows that EBA activity decreased relatively during incorrectly compared to correctly judged trials. It is likely that awareness and attribution of visuomotor in-/congruences depend on a network of connected brain areas (refer to Dehaene et al., 2006), especially in light of a possible disconnection pathology underlying disorders such as schizophrenia. The EBA may be part of a larger network that includes parts of the PPC, the cerebellum and premotor cortex. A dysfunction of such a network may be related to disorders that involve misattributions of agency, such as schizophrenia (Franck et al., 2001; Kircher and Leube, 2003) with dysfunctions of PPC (Spence et al., 1997) and posterior extrastriate cortex (Holzman, 2000).

How can our findings be integrated into the EBA being responsive to body parts? Body parts are our action effectors and it seems likely that a neural representation of body parts encompasses body- and action-related information also in peripersonal space (as suggested by Urgesi et al., 2004; Jeannerod, 2004). Kable and Chatterjee (2006) indeed found evidence for action-specific representations within the EBA. Downing et al. (2006a) suggested that the role of the EBA in action perception might solely be the visual representation of a static structure of the human body rather than anything dynamic or multimodal. In their study (Downing et al., 2006a), the EBA responded more to the visual representation of incoherent than coherent action sequences. However, their results could also be interpreted as the EBA's response to violations of internal action representations as during the perception of incoherent action sequences (as in Downing et al., 2006b) such as during incongruent feedback in the present study. Unfortunately, the present experiment is limited in the sense that it only manipulated visual reafferences. Further investigations, which also manipulate other modalities than only the visual one, are required to test how exactly the body is represented in the EBA and which kinds of violation it may be able to detect.

There were significant differences in RTs to indicate whether a feedback was self- or other-generated: subjects were faster to judge that a movement was self-generated. However, these differences in RT cannot account for differences in EBA activation (Supplementary Fig. 2). Other authors also reported difficulties in subjects' ability to report on visuomotor incongruencies and an over-

attribution of action consequences to the self (e.g., Fourneret and Jeannerod, 1998; see the following references for a more detailed discussion of this result: Jeannerod and Pacherie, 2004; Knoblich and Kircher, 2004; Tsakiris and Haggard, 2005).

It is well established that attention can modulate activation in visual and parietal cortex (Wojciulik et al., 1998; Serences and Yantis, 2006), for example to unexpected stimuli. Unexpected movements of the cursor during incongruent feedback may have introduced a reorienting signal driving the effect of incongruent feedback within the EBA (Downar et al., 2000). However, subjects were instructed to focus on changes in cursor movements. Furthermore, attention may imply awareness of the feedback manipulation, but subjects were not always aware of the mismatch. Nevertheless, additional attentional resources may still have been allocated during incongruent feedback as would be suggested by systematic differences in eye movements (known to influence activity in extrastriate cortex, Freitag et al., 1998). We did not monitor eye movements, but Astafiev et al. (2004) demonstrated that the response in the EBA was specific to movements of the limbs, and did not extend to eye movements. Furthermore, if the response pattern in the EBA was driven purely by attention, we would expect similar patterns of activity in other regions known to be modulated by attention. In contrast, we found that activity in early visual cortex (V1/V2, lingual gyrus and calcarine sulcus; coordinates taken from Astafiev et al., 2004) did not show the same response pattern as did the EBA (Supplementary Fig. 3), neither did regions previously shown to be sensitive to changes in sensory stimuli (as identified by Downar et al., 2000; Supplementary Fig. 4).

Anatomical overlaps of hMT+ and EBA have been reported (Peelen et al., 2006; Spiridon et al., 2006). We did not include an additional functional localizer for hMT+ due to time constraints, thus we cannot absolutely rule out hMT+ influencing the observed effects. However, activation of hMT+ due to increased motion displays during incongruent feedback is not likely as the amount of displayed motion, as well as motion onsets, was balanced across conditions. Moreover, in a recently conducted transcranial magnetic stimulation (TMS) experiment, we found no significant effect of TMS over the EBA on a motion direction detection task (but on the agency task) suggesting that the EBA is not simply critically involved in motion detection (David et al., in press). Nevertheless, two studies reported similar activity profiles of hMT+ and EBA during visually guided movements (Astafiev et al., 2004) and action recognition (Kable and Chatterjee, 2006), which opens the possibility that hMT+, or other regions in occipital–temporal cortex at or near the EBA (Peelen and Downing, 2005), may show similar activations profiles than EBA to a manipulation of agency. This research also demonstrates the need for future fMRI investigations to use improved localization and analysis procedures (e.g., Downing et al., 2007).

To conclude, the present findings suggest a more integrative and dynamic representation of the human body within the EBA. The EBA may detect incongruencies of internal body or action signals and reafferent visual signals, a process that the sense of agency may also rely on, for example, when identifying other agents.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2007.03.030.

References

Astafiev, S.V., Stanley, C.M., Shulman, G.L., Corbetta, M., 2004. Extrastriate body area in human occipital cortex responds to the performance of motor actions. Nat. Neurosci. 7, 542–548.

Astafiev, S.V., Stanley, C.M., Shulman, G.L., Corbetta, M., 2005. Is the extrastriate body area involved in motor actions? Nat. Neurosci. 8, 125–126.

Avikainen, S., Liuhanen, S., Schürmann, M., Hari, R., 2003. Enhanced extrastriate activation during observation of distorted finger postures. J. Cogn. Neurosci. 15, 658–663.

Beauchamp, M.S., 2005. See me, hear me, touch me: multisensory integration in lateral occipital–temporal cortex. Curr. Opin. Neurobiol. 16, 145–153.

Blakemore, S.J., Frith, C.D., 2003. Self-awareness and action. Opin. Neurobiol. 13, 219–224.

Blakemore, S.J., Sirigu, A., 2003. Action prediction in the cerebellum and in the parietal lobe. Exp. Brain Res. 153, 239–245.

Blakemore, S.J., Rees, G., Frith, C.D., 1998. How do we predict the consequences of our actions? A functional imaging study. Neuropsychologia 36, 521–529.

Blakemore, S.J., Frith, C.D., Wolpert, D.M., 2001. The cerebellum is involved in predicting the sensory consequences of action. NeuroReport 12, 1879–1884.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C.A., Rizzolatti, G., 2004. Neural circuits involved in the recognition of actions performed by nonconspecifics: an FMRI study. J. Cogn. Neurosci. 16, 114–126.

Chaminade, T., Decety, J., 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. NeuroReport 13, 1975–1978.

Chan, A.W., Peelen, M.V., Downing, P.E., 2004. The effect of viewpoint on body representation in the extrastriate body area. NeuroReport 15, 2407–2410.

David, N., Bewernick, B.H., Cohen, M.X., Newen, A., Lux, S., Fink, G.R., Shah, N.J., Vogeley, K., 2006. Neural representations of self versus other: visual–spatial perspective taking and agency in a virtual ball-tossing game. J. Cogn. Neurosci. 18, 898–910.

David, N., Jansen, M., Cohen, M.X., Osswald, K., Molnar-Szakas, I., Newen, A., Vogeley, K., Paus, T., in press. Disturbances of self–other distinction after stimulation of the extrastriate body area in the human brain. Social Neuroscience.

Dehaene, S., Changeux, J.P., Naccache, L., Sackur, J., Sergent, C., 2006. Conscious, preconscious, and subliminal processing: a testable taxonomy. Trends Cogn. Sci. 10, 204–211.

Downar, J., Crawley, A.P., Mikulis, D.J., Davis, K.D., 2000. A multimodal cortical network for the detection of changes in the sensory environment. Nat. Neurosci. 3, 277–283.

Downing, P.E., Jiang, Y., Shuman, M., Kanwisher, N., 2001. A cortical area selective for visual processing of the human body. Science 293, 2470–2473.

Downing, P.E., Peelen, M.V., Wiggett, A.J., Tew, B.D., 2006a. The role of the extrastriate body area in action perception. Soc. Neurosci. 1, 52–62.

Downing, P.E., Chan, A.W., Peelen, M.V., Dodds, C.M., Kanwisher, N., 2006b. Domain specificity in visual cortex. Cereb. Cortex 16, 1453–1461.

Downing, P.E., Wiggett, A.J., Peelen, M.V., 2007. Functional magnetic resonance imaging investigation of overlapping lateral occipitotemporal activations using multi-voxel pattern analysis. J. Neurosci. 27, 226–233.

Duvernoy, H.M., 1999. The Human Brain, 2nd ed. Springer, New York.

Ehrsson, H.H., Holmes, N.P., Passingham, R.E., 2005. Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. J. Neurosci. 25, 10564–10573.

Farrer, C., Frith, C.D., 2002. Experiencing oneself vs. another person as being the cause of an action: the neural correlates of the experience of agency. NeuroImage 15, 596–603.

Farrer, C., Franck, N., Georgieff, N., Frith, C.D., Decety, J., Jeannerod, M., 2003. Modulating the experience of agency: a positron emission tomography study. NeuroImage 18, 324–333.

Fourneret, P., Jeannerod, M., 1998. Limited conscious monitoring of motor performance in normal subjects. Neuropsychologia 36, 1133–1140.

Franck, N., Farrer, C., Georgieff, N., Cardine, M., Dalery, J., d'Amato, T., Jeannerod, M., 2001. Defective recognition of one's own actions in patients with schizophrenia. Am. J. Psychiatry 158, 454–459.

Freitag, P., Greenlee, M.W., Lacina, T., Scheffler, K., Radü, E.W., 1998. Effect of eye movements on the magnitude of functional magnetic resonance imaging responses in extrastriate cortex during visual motion perception. Exp. Brain Res. 119, 409–414.

Friston, K.J., Buchel, C., Fink, G.R., Morris, J., Rolls, E., Dolan, R.J., 1997. Psychophysiological and modulatory interactions in neuroimaging. NeuroImage 6, 218–229.

Gallagher, S, 2000. Philosophical conceptions of the self: implications for cognitive science. Trends Cogn. Sci. 4, 14–21.

Haggard, P., Whitford, B., 2004. Supplementary motor area provides an efferent signal for sensory suppression. Brain Res. Cogn. Brain Res. 19, 52–58.

Hamilton, A.F., Wolpert, D.M., Frith, U., Grafton, S.T., 2005. Where does your own action influence your perception of another person's action in the brain? NeuroImage 29, 524–535.

Holzman, P.S., 2000. Eye movements and the search for the essence of schizophrenia. Brain Res. Rev. 31, 350–356.

Iacoboni, M., Koski, L.M., Brass, M., Bekkering, H., Woods, R.P., Dubeau, M.C., Mazziotta, J.C., Rizzolatti, G., 2001. Reafferent copies of imitated actions in the right superior temporal cortex. Proc. Natl. Acad. Sci. U. S. A. 98, 13995–13999.

Jackson, P.L., Decety, J., 2004. Motor cognition: a new paradigm to study self–other interactions. Curr. Opin. Neurobiol. 14, 259–263.

Jackson, P.L., Meltzoff, A.N., Decety, J., 2006. Neural circuits involved in imitation and perspective-taking. NeuroImage 31, 429–439.

Jeannerod, M., 1999. The 25th Bartlett Lecture. To act or not to act: perspectives on the representation of actions. Q. J. Exp. Psychol., A 52, 1–29.

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

Jeannerod, M., Pacherie, E., 2004. Agency, simulation and self-identification. Mind Lang. 19, 113–146.

Kable, J.W., Chatterjee, A., 2006. Specificity of action representations in the lateral occipitotemporal cortex. J. Cogn. Neurosci. 18, 1498–1517.

Kircher, T.T., Leube, D.T., 2003. Self-consciousness, self-agency, and schizophrenia. Conscious. Cogn. 12, 656–669.

Knoblich, G., Kircher, T.T., 2004. Deceiving oneself about being in control: conscious detection of changes in visuomotor coupling. J. Exp. Psychol. Hum. Percept. Perform. 30, 657–666.

Lau, H.C., Rogers, R.D., Haggard, P., Passingham, R.E., 2004. Attention to intention. Science 303, 1208–1210.

Leube, D.T., Knoblich, G., Erb, M., Grodd, W., Bartels, M., Kircher, T.T., 2003. The neural correlates of perceiving one's own movements. NeuroImage 20, 2084–2090.

Lewis, J.W., Van Essen, D.C., 2000. Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. J. Comp. Neurol. 428, 112–137.

MacDonald, P.A., Paus, T., 2003. The role of parietal cortex in awareness of

self-generated movements: a transcranial magnetic stimulation study. Cereb. Cortex 13, 962–967.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. NeuroImage 19, 1233–1239.

Miall, R.C., 2003. Connecting mirror neurons and forward models. NeuroReport 14, 2135–2137.

Nielsen, T., 1963. Volition: a new experimental approach. Scand. J. Psychol. 4, 225–230.

Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9, 97–113.

Oreja-Guevara, C., Kleiser, R., Paulus, W., Kruse, W., Seitz, R.J., Hoffmann, K.P., 2004. The role of V5 (hMT+) in visually guided hand movements: an fMRI study. Eur. J. Neurosci. 19, 3113–3120.

Pacherie, E., 2001. Agency lost and found: a commentary on Spence. Philos. Psychiatry Psychol. 8, 173–176.

Peelen, M.V., Dowing, P., 2005. Is the extrastriate body area involved in motor actions? Nat. Neurosci. 8, 125.

Peelen, M.V., Downing, P.E., 2005. Within-subject reproducibility of category-specific visual activation with functional MRI. Hum. Brain. Mapp. 25, 402–408.

Peelen, M.V., Wiggett, A.J., Downing, P.E., 2006. Patterns of fMRI activity dissociate overlapping functional brain areas that respond to biological motion. Neuron 49 (6), 815–822.

Ramnani, N., Miall, R.C., 2004. A system in the human brain for predicting the actions of others. Nat. Neurosci. 7, 85–90.

Rilling, J.K., Sanfey, A.G., Aronson, J.A., Nystrom, L.E., Cohen, J.D., 2004. The neural correlates of theory of mind within interpersonal interactions. NeuroImage 22, 1694–1703.

Ruby, P., Decety, J., 2001. Effect of subjective perspective taking during simulation of action: a PET investigation of agency. Nat. Neurosci. 4, 546–550.

Saxe, R., Jamal, N., Powell, L., 2006. My body or yours? The effect of visual perspective on cortical body representations. Cereb. Cortex 16, 178–182.

Schenk, T., Mai, N., Ditterich, J., Zihl, J., 2000. Can a motion-blind patient reach for moving objects? Eur. J. Neurosci. 12, 3351–3360.

Schnell, K., Heekeren, K., Schnitker, R., Daumann, J., Weber, J., Hesselmann, V., Möller-Hartmann, W., Thron, A., Gouzoulis-Mayfrank, E., 2007. An fMRI approach to particularize the frontoparietal network for visuomotor action monitoring: detection of incongruence between test subjects' actions and resulting perceptions. NeuroImage 34, 332–341.

Serences, J.T., Yantis, S., 2006. Selective visual attention and perceptual coherence. Trends Cogn. Sci. 10, 38–45.

Sirigu, A., Daprati, E., Pradat-Diehl, P., Franck, N., Jeannerod, M., 1999. Perception of self-generated movement following left parietal lesion. Brain 122 (Pt 10), 1867–1874.

Slachevsky, A., Pillon, B., Fourneret, P., Pradat-Diehl, P., Jeannerod, M., Dubois, B., 2001. Preserved adjustment but impaired awareness in a sensory-motor conflict following prefrontal lesions. J. Cogn. Neurosci. 13, 332–340.

Spence, S.A., Brooks, D.J., Hirsch, S.R., Liddle, P.F., Meehan, J., Grasby, P.M., 1997. A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control). Brain 120, 1997–2011.

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.

Synofzik, M., Vosgerau, G., Newen, A., in press. Beyond the comparator model: A multifactorial two-step account of agency. Conscious. Cogn.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Georg Thieme, Stuttgart.

Tsakiris, M., Haggard, P., 2005. Experimenting with the acting self. Cogn. Neuropsychol. 22, 387–407.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage 15, 273–289.

Ungerleider, L.G., Desimone, R., 1986. Cortical connections of visual area MT in the macaque. J. Comp. Neurol. 248, 190–222.

Urgesi, C., Berlucchi, G., Aglioti, S.M., 2004. Magnetic stimulation of extrastriate body area impairs visual processing of nonfacial body parts. Curr. Biol. 14, 2130–2134.

Wegner, D.M., Sparrow, B., Winerman, L., 2004. Vicarious agency: experiencing control over the movements of others. J. Pers. Soc. Psychol. 86, 838–848.

Wojciulik, E., Kanwisher, N., Driver, J., 1998. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. J. Neurophysiol. 79, 1574–1578.

Wolpert, D.M., Ghahramani, Z., Jordan, M.I., 1995. An internal model for sensorimotor integration. Science 269, 1880–1882.